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Distribution ecology of the harpy eagle: spatial patterns and processes to direct conservation planning

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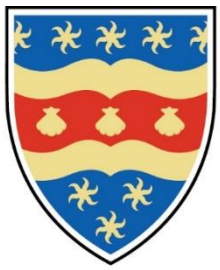

UNIVERSITY OF PLYMOUTH

DISTRIBUTION ECOLOGY OF THE HARPY EAGLE: SPATIAL PATTERNS AND PROCESSES TO DIRECT CONSERVATION PLANNING.

by

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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'It's tough to make predictions, especially about the future'.

- Mark Twain

Luke James Sutton

Distribution ecology of the harpy eagle: spatial patterns and processes to direct conservation planning.

Abstract

Accurately demarcating species distributions has long been at the core of ecology. Yet our understanding of the factors limiting species range limits is incomplete, especially for tropical species. Human-driven threats to the survival of many taxa are increasing, particularly habitat loss and climate change. Identifying distributional range limits of at-risk species can thus inform spatial conservation planning to mitigate these threats. The harpy eagle (*Harpia harpyja*) is a large raptor distributed across Neotropical lowland forests, from southern Mexico to northern Argentina, currently threatened by habitat loss and persecution. Coupled with climate change, harpy eagle distribution may contract or shift leading to uncertainty on its future conservation. Here, I use point process regression models and ordination to identify harpy eagle environmental range limits and recommend spatial conservation planning measures for the species. I propose a revised range size 11 % smaller and an Extent of Occurrence 26 % less than the current estimates. By including biotic interactions in model predictions, I show that prey resources are more important for limiting harpy eagle distribution than climatic conditions. When compared to crested eagle (*Morphnus guianensis*) distribution, the harpy eagle's primary competitor, both species shared identical habitat resource space, with only subtle differences in distribution. Range-wide habitat use indicated that harpy eagles prefer areas of 70-75 % evergreen forest cover, low elevation and high vegetation heterogeneity, but avoid cultivated land, mosaic forest and complex topography. The current Important Bird and Biodiversity Area (IBA) network covered 17 % of medium to high harpy eagle habitat exceeding the protected area target representation (10 %). Under a future high emissions climate change scenario, range size was predicted to decrease by 14.4 % by 2090, with the IBA network covering 14 % less of its current coverage. Despite its large range, the harpy eagle has specialized habitat requirements and would benefit from targeted conservation measures based on spatial models in order to maintain viable populations.

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1. Introduction

1.1 Background

Mapping geographic ranges and identifying environmental requirements of individual species are fundamental research areas in conservation biogeography (Riddle *et al.* 2011). Defining species' spatial and ecological range limits is essential to assess the various threats facing many taxa in rapidly changing environments (Ladle & Whittaker 2011), and to formulate viable conservation plans for species survival (Margules & Pressey 2000). However, significant knowledge gaps still exist on the full area of distribution and environmental attributes of where individual species occur, commonly termed the 'Wallacean Shortfall' (Lomolino 2004). The Wallacean Shortfall contributes to a second knowledge deficit where, if the current range of a species is unknown or not fully described, it is not possible to determine whether and when a species is in decline or possibly gone extinct. There is therefore uncertainty in whether any future predicted range losses or contractions are higher than background extinction levels (Riddle *et al.* 2011).

Understanding which environmental factors limit the distribution and abundance of broad-ranged species is still poorly understood (Ghergel *et al.* 2018). The current paradigm is that climate plays a central role in determining species distributions at continental scales (Pearson & Dawson 2003; Peterson *et al.* 2011; Franklin 2013). However, recent work has demonstrated that biotic interactions (Aragón *et al.* 2018; Ghergel *et al.* 2018), landcover (Tuanmu & Jetz 2014, 2015) and topography (Meineri & Hylander 2017) are also important at setting range limits for broad-ranged taxa. Species Distribution Models (SDMs) are a group of geospatial statistical methods that assess species'

habitat requirements and predict distribution based on correlating environmental covariates with species occurrences (Franklin 2009). For broad-ranged species that exist in remote, hard to survey areas, SDMs may be an effective method to estimate distribution using environmental layers generated from Geographic Information Systems (GIS) coupled with online biodiversity inventory data from sources such as museums, atlases and community science projects (Bradter *et al.* 2017). Despite issues of sampling bias in opportunistically collected inventory data (Franklin 2009), such data often cover a large sampling extent beyond what would be possible from systemically sampling across continental scales. Thus, with improved modelling methods able to account for inherent spatial biases, such as point process models (PPMs, Renner *et al.* 2015), biodiversity inventory data can help fill distribution knowledge gaps.

1.2 Study species and rationale

The harpy eagle (*Harpia harpyja*) is a large raptor (Fig. 1.1), with a broad distribution across lowland tropical forests in Central and South America from southern Mexico to northern Argentina (Fig. 1.2; Ferguson-Less & Christie 2005; BirdLife International 2017). The species is classified as 'Near Threatened' on the International Union for Conservation of Nature (IUCN) Red List (Birdlife International 2017), but is considered endangered or locally extinct in some parts of its range, notably in Central America (Vargas González *et al.* 2006) and Brazil's Atlantic Forest (Meller & Guadagnin 2016). However, restoration and captive breeding projects have had some success reintroducing harpy eagles to parts of Central America where they have been extirpated (Muela & Curti 2005; Watson *et al.* 2016).

Figure 1.1. Adult harpy eagle (*Harpia harpyja*) showing distinct feathered ‘crown’ on the top of the head and large feet for capturing arboreal mammal prey.

Harpy eagles generally prefer uninterrupted expanses of lowland tropical forest, with habitat loss and fragmentation the primary threats to the species future persistence (Vargas González *et al.* 2006). However, the environmental determinants of harpy eagle distribution and abundance are still largely unknown. Spatial modelling can therefore help determine the essential ecological requirements of the harpy eagle, currently identified as a priority area of research by the IUCN (BirdLife International 2017). Further, predicting the distributional potential for the harpy eagle across current, historical, and future timescales would enable specific hypotheses to be developed and tested on the processes limiting its distribution, along with directing current field sampling

Figure 1.2. Current estimate of harpy eagle (*Harpia harpyja*) distribution based on the latest assessment from the International Union for Conservation of Nature (IUCN) and BirdLife International (2017).

protocols to identify potential areas of occupation (Peterson & Anamza 2015). Improving the predictive power of spatial models by incorporating biotic, landcover, and topographical predictors would also lead to higher certainty on where to designate new and strengthen existing protected area networks (Elith

& Leathwick 2009a; Lawler *et al.* 2011). Such modelling goals include predicting the core remaining areas of habitat at both the regional and continental level to identify priority areas for current spatial conservation planning and direct future research on the impacts of climate change.

Anthropogenic climate change is predicted to have a significant impact on the distribution and viability of many avian populations into the future (Şekercioğlu *et al.* 2008; Pearce-Higgins & Green 2014). In tropical regions where precipitation may be the most important determinant of avian distributions (Şekercioğlu *et al.* 2012), climate change may not necessarily result in poleward range shifts but in multi-directional range shifts (VanDerWal *et al.* 2013). Within the Neotropical avifauna, hawks and eagles (Accipitridae) may be particularly affected by climate change, because they generally exist at low population densities and are sensitive to habitat loss and fragmentation (Newton 1979; Stotz *et al.* 1996; Krüger & Radford 2008). Therefore, the potentially negative consequences of climate change may add another threat to the harpy eagle which is already existing in challenging conditions. However, currently no assessment has been made on the effect of climate change on harpy eagle distribution, and the amount and location of suitable future climate space for the species.

A recent review on the status of global raptor species estimated that 52 % of raptors were declining globally (McClure *et al.* 2018). South America was identified in the top three continental regions with highest raptor species richness, but with the most threatened and declining raptor species. Further, tropical forest raptor species are more threatened compared to non-tropical

forest species. Based on models of deforestation in the Amazon basin, the harpy eagle is estimated to lose between 28-46 % of habitat over three generations, or 56 years (Soares-Filho *et al.* 2006; Bird *et al.* 2012). Defining the distributional constraints for harpy eagles can thus identify the most suitable areas of current climate and habitat, hind-cast past distribution to identify areas of long-term climatic stability and predict future distribution under expected climate change scenarios. Applying this knowledge to current and future conservation management can then direct designation of the current network of protected areas in line with suitable environmental areas now and into the future.

Given this background the aims of this thesis are to identify current, past, and future distributions for the harpy eagle, and apply spatial analysis and predictive modelling to estimate distribution and identify environmental range limits. The key objective is to use this information to inform current spatial conservation planning and predict future climate change impacts on distribution across the harpy eagle range. The thesis is divided into seven chapters:

Chapter 1: Introduction

Chapter 2: Geographic range estimates and environmental requirements for the harpy eagle derived from spatial models of current and past distribution

Chapter 3: Prey resources are more important than abiotic conditions for predicting the distribution of a broad-ranged apex predator

Chapter 4: Habitat resource overlap in two sympatric Neotropical forest eagles

Chapter 5: Range-wide habitat use and protected area coverage in a tropical forest raptor population within an increasingly deforested landscape

Chapter 6: Reduced range size and protected area coverage for the harpy eagle predicted from multiple climate change scenarios

Chapter 7: Conclusion

Chapter 2 sets out baseline estimates for current distribution based on climate and topography and predicts range size and extent at two paleoclimate time periods. By incorporating prey resource distributions in the modelling, in Chapter 3 I test the long-standing biogeographic paradigm that climate is the key driver for broad-ranged species distributions. Chapter 4 compares habitat resource overlap between the harpy eagle and its nearest genetic relative, the crested eagle (*Morphnus guianensis*), and combines both species occurrences in a single habitat model. In Chapter 5 I identify range-wide habitat use by the harpy eagle, estimate protected area coverage and conduct a gap analysis to identify priority areas to designate new protected areas. In Chapter 6 I predict future distribution based on multiple climate change scenarios between the years 2030-2090 and determine how climate change may affect protected area coverage within the harpy eagle distributional range. Finally, chapter 7 draws together the general conclusions of the study.

2. Geographic range estimates and environmental requirements for the harpy eagle derived from spatial models of current and past distribution

2.1 Abstract

Understanding species-environment relationships is key to defining the spatial structure of species distributions and develop effective conservation plans. However, for many species this baseline information does not exist. With reliable presence data, spatial models that predict geographical ranges and identify environmental processes regulating distribution are a cost-effective and rapid method to achieve this. Yet these spatial models are lacking for many rare and threatened species, particularly in tropical regions. The harpy eagle (*Harpia harpyja*) is a Neotropical forest raptor of conservation concern, with a continental distribution across lowland tropical forests in Central and South America. Currently the harpy eagle faces threats from habitat loss and persecution and is categorised as Near-Threatened by the International Union for the Conservation of Nature (IUCN). Within a point process modelling (PPM) framework, I use presence-only occurrences with climatic and topographical predictors to estimate current and past distributions and define environmental requirements using Ecological Niche Factor Analysis. The current PPM model had high calibration accuracy (Continuous Boyce Index = 0.838) and was robust to null expectations (pROC ratio = 1.407). Three predictors contributed 96 % to the PPM prediction, with Climatic Moisture Index the most important (72.1 %), followed by minimum temperature of the warmest month (15.6 %) and Terrain Roughness Index (8.3 %). Assessing distribution in environmental space confirmed the same predictors explaining distribution, along with precipitation in the wettest month. The reclassified binary model estimated a

current range size 11 % smaller than the current IUCN range polygon. Paleoclimatic projections combined with the current model predicted stable climatic refugia in the central Amazon, Guyana, eastern Colombia, and Panama. I propose a data-driven geographical range to complement the current IUCN range estimate, and that despite its continental distribution this tropical forest raptor is highly specialized to specific environmental requirements.

2.2 Introduction

Defining species distributions in geographical and environmental space is a fundamental component of conservation management (Peterson *et al.* 2011). Yet this information is lacking for many rare and threatened taxa in a rapidly changing environment (Miller 2010; Lawler *et al.* 2011). Assessing geographic distribution and environmental requirements of rare and poorly studied species can be problematic due to scarce occurrence data, resulting in limited information for conservation managers to act upon (Pearce & Boyce 2006). For these under-documented species this baseline spatial information is either inadequate, or non-existent, especially in highly biodiverse tropical regions, often where organismal biology is also poorly known (Rodríguez *et al.* 2007; Tobias *et al.* 2013; Wilson *et al.* 2016, Buechley *et al.* 2019). In response to this knowledge gap, spatial modelling techniques have been developed to help direct conservation actions and implement research programs.

Species Distribution Models (SDMs) can overcome deficiencies in information regarding distribution by correlating the underlying environmental data at known occurrences to predict the areas of highest environmental suitability (Scott *et al.* 2002; Elith & Leathwick 2009b). On the other hand, ordination approaches

define the underlying environmental factors that explain the most suitable environmental conditions for where a given species is found. Combining both SDMs and ordination is an effective method to define the distributional and ecological constraints of a given species (Chase & Leibold 2003; Soberón & Nakamura 2009; Peterson *et al.* 2011). These methods are particularly useful when using species occurrences generated from biodiversity databases when modelling distributions for species in remote, difficult to survey regions (Peterson 2001; Rhoden *et al.* 2017; Sutton & Puschendorf 2018).

The Neotropics are well-known for high avian biodiversity. Yet many birds, including raptors, face multiple threats across the area, largely driven by human activities such as habitat loss, agricultural development and resource over-exploitation (Tobias *et al.* 2013; Sarasola *et al.* 2018, McClure *et al.* 2018, Buechley *et al.* 2019). Due to the difficulties of sampling across the extensive and complex terrain of the Neotropics, applying SDMs using open-access distribution data can generate baseline information on species distributions in a rapid and cost-effective manner (Cayuela *et al.* 2009; La Sorte & Somveille 2020). The harpy eagle (*Harpia harpyja*) is a large Neotropical raptor, with a broad yet shrinking range across Central and South America from southern Mexico to northern Argentina (Ferguson-Lees & Christie 2005; Vargas González *et al.* 2006). Harpy eagles generally occur at low population densities in lowland tropical forest (Vargas González & Vargas 2011) but are nearly extinct in Brazil's Atlantic forest (Srbek-Araujo & Chiarello 2006; Meller & Guadagnin 2016) and in forest enclaves such as riparian forests in open savannahs (Silva *et al.* 2013).

With generally low population densities and a 3-year long breeding cycle, the harpy eagle is considered a species of conservation concern due to continued habitat loss and persecution (Vargas González *et al.* 2006; Miranda *et al.* 2019). Currently categorised as 'Near-Threatened' by the International Union for the Conservation of Nature (IUCN; Birdlife International 2017), local extirpations have occurred in most of Central America, and the population status of the species across its continental range is largely unknown (Vargas González *et al.* 2006). The current IUCN geographic range for the harpy eagle estimates an Extent of Occurrence (EOO) of 17.6 million km^2 and an unknown Area of Occupancy (AOO, Birdlife International 2017). EOO measures the area within a minimum convex polygon (MCP) from all known species occurrences, while AOO is a subset of the EOO where the species actually occurs in occupied grid cells of 2x2 km, excluding vagrancy (Gaston & Fuller 2009; Brooks *et al.* 2019). Both measures are based solely on spatial locations and not on underlying environmental information.

One of the main criticisms of using EOO is that it often includes unsuitable areas, overestimating the true range, which is more likely to show a discontinuous pattern of distribution (Jetz *et al.* 2007; Peterson *et al.* 2016; Breiner *et al.* 2017; Ramesh *et al.* 2017). SDMs are useful as an alternative measure to complement IUCN estimates, intermediate between EOO and AOO, especially for rare and under-sampled species (Breiner *et al.* 2017). SDMs should not be viewed as surrogates for IUCN criteria but can provide a basis for estimating AOO (Gaston & Fuller 2009; Breiner *et al.* 2017; IUCN 2019), especially in the case for the harpy eagle where this figure is unknown. Using the underlying environmental signature of the species as a guide for model

interpolation may produce a more realistic data-driven estimate of distribution area (Peterson *et al.* 2016). Global range size is a key parameter for assessing threat status and extinction risk, thus overestimating this figure could lead to increasingly threatened species being missed (Ramesh *et al.* 2017). Predicting areas with the highest environmental suitability can thus focus research effort and update threatened species' conservation status (Bierregaard 1998).

Miranda *et al.* (2019) produced the first SDM for the harpy eagle, identifying its close relationship to lowland tropical forest. This study builds on the strengths of this initial SDM, first by incorporating extra presence-only occurrences with the Miranda *et al.* location data, and second using an expanded set of environmental predictors. Additionally, current predictions are projected into two paleoclimatic scenarios and predict how past distributions may influence present and future distribution. Long-term ecological perspectives from paleoclimate models are important for comparing current distribution to past fluctuations (Nogués-Bravo 2009; Fuller *et al.* 2011). Further, having a long-term perspective of past distributions is critical to interpreting current distribution and can point towards potential refugia expected from future changes in range size (Fuller *et al.* 2011; Keppel *et al.* 2012). Understanding the species-environment relationships regulating current and historical harpy eagle distribution can therefore help direct conservation management by identifying the spatial extent for the species.

Here, I develop predictive spatial models for the harpy eagle in geographical space using a point process modelling (PPM) framework. Recently, PPMs have been shown to be most effective for modelling distributions using presence-only

occurrences (Warton & Shepherd 2010; Renner *et al.* 2015). PPMs model the intensity of occurrence points across a given area, thus under low spatial dependence of occurrences the resulting outputs can be interpreted as either the relative (Renner *et al.* 2015), or potential abundance of focal species (Phillips *et al.* 2017). An ecological profile is then developed using ordination with an Ecological Niche Factor Analysis (ENFA) to best explain the environmental requirements of the harpy eagle, compared to the background environmental conditions available. Specifically, I aim to: **(1)** re-evaluate current harpy eagle distribution and establish its ecological niche as a function of climatic and topographical predictors, **(2)** revise the estimated current coarse-scale IUCN distributional area and provide complementary range maps, and **(3)** predict past distributions from two paleoclimatic time periods and combine with the current model to identify stable refugia.

2.3 Methods

2.3.1 Harpy Eagle occurrence data

Harpy eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, The Peregrine Fund 2018) a data information system for all raptor species. For the harpy eagle, GRIN consists of occurrence data from the Global Biodiversity Information Facility (GBIF 2019a), which are mostly eBird records (79 %, Sullivan *et al.* 2009), combined with two additional datasets of nests and observations (Vargas González & Vargas 2011; Miranda *et al.* 2019). Occurrence data were cleaned by removing duplicate records, those with no geo-referenced location and for spatial auto-correlation. To account for sampling bias in occurrences, a 4 km spatial filter from each occurrence point was used to minimise the effects of survey bias, using the 'thin' function in the R package spThin (Aiello-Lammens *et al.* 2015). The 4 km thinning distance was selected as a proxy of mean inter-nest distances based on breeding pairs in the Darien region of Panama (Vargas González & Vargas 2011). I used 4 km as a minimum distance knowing that inter-nest distances recorded across the harpy eagle range can vary (Piana 2007; Muñiz-López 2008).

Spatial auto-correlation in occurrence data was measured using Global Moran's *I* index on an inverse Euclidean distance matrix projected into Lambert Azimuth Equal Area (LAEA) for South America using the R package ape (Paradis *et al.* 2004). Moran's *I* is an index ranging from -1 to +1, with values closer to zero indicating no spatial auto-correlation, and values approaching the extremes indicating stronger negative or positive autocorrelation, respectively. Spatial clustering was measured using Nearest Neighbour Index (NNI) in the R package spatialEco (Evans 2018) with a convex hull window. NNI is the ratio of

the observed distance divided by the expected distance between neighbours in a hypothetical random distribution. NNI < 1 indicates spatial clustering, with values of 1 indicating random dispersion, and those closer to 2 indicating regular dispersion.

After data cleaning, a total of 1179 geo-referenced records were compiled for inclusion in model calibration, generally within the current range defined by the IUCN (Fig. S2.1; Birdlife International 2017). Cleaned occurrence data were spatially auto-correlated (Moran's I = 0.808, p < 0.001) and showed spatial clustering (NNI = 0.333, z = -43.794, p < 0.001). After applying the 4km spatial filter, spatial auto-correlation was reduced (Moran's I = 0.534, p < 0.001), with clustering moving towards random dispersion (NNI = 0.492, z = -26.471, p < 0.001) resulting in 742 spatially-filtered occurrence records for use in the calibration models (Fig. S2.2; mean elevation = 264 m, range = 2 - 2177 m). The resulting occurrence points are thus best reported as locations in continuous space, providing the primary motivation for using the PPM regression framework for subsequent spatial analysis (Renner *et al.* 2015).

2.3.2 Environmental predictors

Thirty-seven bioclimatic and topographical predictors were obtained from the WorldClim (v1.4, Hijmans *et al.* 2005) and ENVIREM (Title & Bemmels 2018) databases. WorldClim variables (n = 19) are generated through interpolation of average monthly weather station climate data from 1960-1990. The ENVIREM dataset includes 16 climatic and two topographic variables to complement the WorldClim dataset providing a wider range of potential variables from which to select model predictors. Incorporating the ENVIREM variables into SDMs can

improve model performance, with the additional variables having direct links to species biology (Title & Bemmels 2018). Raster layers were cropped and masked to a delimited polygon consisting of all known range countries (including the states of Formosa, Jujuy, Misiones and Salta in northern Argentina, and the states of Chiapas, Oaxaca, and Tabasco in southern Mexico), to extend into potential areas of marginal habitat on the distribution edges. Reducing the accessible area to the known range improves model predictive power by reducing the background area used for testing points used in model evaluation (Barve *et al.* 2011; Radosavljevic & Anderson 2014).

For past predictions, three General Circulation Models (GCMs, Table 2.1) were used from the Coupled Model Inter-comparison Project Phase 5 (CMIP5) and Paleoclimate Modelling Inter-comparison Project Phase 3 (PMIP3) databases for two paleoclimate scenarios in the Mid-Holocene (~6,000 calendar years before present) and Last Glacial Maximum (~22,000 cal. yr. BP). Three GCMs were used to account for variation and uncertainty in model predictions (Nogués-Bravo 2009), and a mean prediction calculated from all models for both paleoclimate scenarios. Each summed paleo-distribution was then stacked with the current distribution and overlaid to provide a summed estimate of environmental stability (Peterson *et al.* 2017), using the 'stability' function in the R package 'sdStaf' (Atauchi 2018). Summed stability can predict areas of stable refugia, where a species is predicted to be present irrespective of time period (Carnaval *et al.* 2009). Geographic niche overlap from the individual GCMs was tested using Schoener's *D* (Schoener 1968, Warren *et al.* 2008), which ranges between 0 (no overlap) to 1 (identical overlap). Paleoclimate raster data were downloaded from the WorldClim (version 1.4, Hijmans *et al.* 2005) and

ENVIREM (Title & Bemmels 2018) databases and masked to the current range extent to predict areas of past climatic suitability compared to the current range.

Table 2.1. General Circulation Models (GCMs) from the Coupled Model Inter-comparison Project Phase 5 (CMIP5) and Paleoclimate Modelling Inter-comparison Project Phase 3 (PMIP3) databases used to predict past distributions for two paleoclimate scenarios in the Mid-Holocene (~6,000 cal. yr. BP) and Last Glacial Maximum (~22,000 cal. yr. BP).

GCM	Acronym	Citation
Community Climate System Model, v4	CCSM4	Gent *et al.* 2011
Model for Interdisciplinary Research on Climate – Earth System Model	MIROC-ESM	Watanabe *et al.* 2011
Max Planck Institute for Meteorology – Earth System Model - Paleo	MPI-ESM-P	Giorgetta *et al.* 2013

Multicollinearity between environmental predictor variables can bias models by over-representing the biological relevance of correlated variables (Franklin 2009; Phillips *et al.* 2006). Before model construction, environmental cells containing occurrence records from all 37 variables were tested for multicollinearity using Variance Inflation Factor (VIF) analysis (Guisan *et al.* 2006; Hair *et al.* 2006) with the 'corSelect' function in the R package fuzzySim (Barbosa 2015, 2018). VIF is based on the square of multiple correlation coefficients, regressing a single predictor variable against all other predictors. VIF tests can detect hidden correlations in predictors not always apparent in pair-wise correlations. A stepwise elimination of highly correlated variables was used retaining predictors with a VIF threshold < 10, considered as suitable for multi-variable correlation (Dormann *et al.* 2013). The remaining variables were then checked for collinearity using Spearman's Correlation Coefficient with only variables $r_s \leq |0.7|$ retained for consideration as predictors. Only climatic and

topographical predictors were used as based on current knowledge there are no reliable estimates of landcover extent or anthropogenic impact extending back to the two paleoclimate scenarios used here.

After removing highly correlated variables, eight climatic variables (isothermality; maximum temperature warmest month; precipitation wettest month; precipitation warmest quarter; Climatic Moisture Index (CMI); minimum temperature warmest month, potential evapotranspiration (PET) driest quarter; PET wettest quarter), and one topographic variable, Terrain Roughness Index (TRI), were included as predictors at a spatial resolution of 2.5 arc-minutes (~4.5km resolution). Final predictor selection was based on representing monthly and seasonal climatic trends, extremes and limiting environmental factors strongly related theoretically and empirically to species distributions (Stockwell 2006; Bradie & Leung 2017; Guevara *et al.* 2018). For example, in tropical forests rainfall regime and seasonality are predicted to have a strong effect on avian survival, food availability, and reproductive effort (Stotz *et al.* 1996; Williams & Middleton 2008). Therefore, predictors were selected based on seasonal and monthly extremes of precipitation interacting with temperature, as potential limiting factors on harpy eagle distribution (Williams & Middleton 2008; Busch *et al.* 2011).

Isothermality quantifies variation of annual temperatures using the size of oscillation between day-night temperatures relative to annual temperatures and is a useful predictor for tropical species (Nix 1986). Isothermal values < 100 indicate low levels of temperature variability within an average month relative to the year. Climatic Moisture Index (CMI) is a scaled measure ($-1 \leq CMI \leq 1$) of

the ratio of annual precipitation and annual evapotranspiration (Willmott & Feddema 1992). Two variables of seasonal potential evapotranspiration (PET) were included as proxies for vegetation greenness, ultimately determined by ambient energy (Currie 1991). Terrain Roughness Index (TRI) is a measure of variation in topography around a central pixel, with lower values indicating flat terrain and higher values indicating larger differences in elevation of neighbouring pixels (Wilson *et al.* 2007). Terrain complexity and variability can be an important determinant of species distributions and may be viewed as a surrogate for habitat variability because rougher topography is often associated with variation in habitat (Riley *et al.* 1999). As the harpy eagle generally prefers flatter, lowland areas (Vargas González & Vargas 2011), including TRI should be an important predictor with an expected harpy eagle preference for areas with lower TRI values.

2.3.3 Species Distribution Models

SDMs were fitted using a point process modelling (PPM) framework as a form of infinitely-weighted logistic regression via penalized maximum likelihood (Fithian & Hastie 2013), treating occurrences as points rather than grid cells in the R package maxnet (Phillips *et al.* 2017) and maximum entropy software, MAXENT (v3.4.1). Recent theoretical work has demonstrated the equivalence of MAXENT to an inhomogeneous Poisson process (IPP; Fithian & Hastie 2013; Renner & Warton 2013; Renner *et al.* 2015), which is the most appropriate method for fitting presence-only SDMs (Warton & Shepherd 2010). The complementary log-log (cloglog) transform was selected as a continuous index of environmental suitability, with 0 = low suitability and 1 = high suitability. Phillips *et al.* (2017) demonstrated the cloglog transform is equivalent to an IPP

and can be interpreted as a measure of relative occurrence probability proportional to a species relative abundance.

A random sample of 10,000 background points was used as pseudo-absences recommended for regression-based modelling (Barbet-Massin *et al.* 2012) and to sufficiently sample the background calibration environment (Guevara *et al.* 2018). Convergent threshold was set at 10^{-5} and iterations increased to 5000 from the default (500) allowing for model convergence. Optimal-model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich &Tsai 1989), to determine the most parsimonious model by tuning two key MAXENT parameters: regularization multiplier and feature classes (Warren & Seifert 2011). Eighteen candidate models of varying complexity were built by comparing a range of regularization multipliers from 1 to 5 in 0.5 increments, and two feature classes (Linear and Quadratic terms) in all possible combinations using the 'checkerboard2' method of cross-validation (*k*-folds = 5) within the ENMeval package in R (Muscarella *et al.* 2014).

Only Linear and Quadratic features were considered to produce less complex and more realistic predictions (Merow *et al.* 2013; Guevara *et al.* 2018). Omitting Threshold and Product feature classes generally results in increased model performance and more biologically meaningful model interpretations (Phillips *et al.* 2017). Hinge features were used in calibration models, but resulted in biologically unrealistic response curves, and were therefore omitted. The checkerboard cross-validation method of partitioning masks the geographical structure of the data according to latitudinal and longitudinal lines, dividing all occurrences into four spatially independent bins of equal numbers.

By masking the geographical structure of test data, the models are projected onto an evaluation region not included in the calibration process. All occurrence and background test points are assigned to their respective bins dependent on location, thus further reducing spatial auto-correlation between testing and training localities (Radosavljevic & Anderson 2014).

2.3.4 Model evaluation

Optimal model selection was evaluated using Area Under the Curve (AUC), and omission rates. AUC is a non-parametric, threshold-independent measure with AUC = 1.0 indicating maximum predictive performance, and AUC = 0.5 being no better than a random prediction. AUC_{DIFF} (AUC_{TRAIN} - AUC_{TEST}) was used to quantify model over-fitting (Muscarella *et al.* 2014), with a value close to zero indicating a low over-fit model (Warren & Seifert 2011). AUC metrics were used as a measure of optimal model selection, best suited to comparing a range of candidate models (Lobo *et al.* 2008; Jiménez-Valverde 2012). Omission rates are threshold-dependent metrics for evaluating discriminatory ability and over-fitting at specified thresholds. Lower omission rates show improved discrimination between suitable and unsuitable areas (indicating higher performance), whilst overfitted models show higher omission rates than expected by theory (Radosavljevic & Anderson 2014). Omission rates were calculated based on two threshold rules: minimum training presence (MTP) and 10% training presence (10TP). For low over-fit models the expectation in MTP is a value close to zero and for 10TP a value close to 0.10.

Two further test metrics were used to evaluate the final best-fit model. First, model accuracy was tested against random expectations using partial receiver

operating characteristic (pROC), which estimates model performance by giving precedence to omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios range from 0 – 2 with 1 indicating a random model. Function parameters were set with a 5% omission error rate, and 1000 bootstrap replicates on 50% test data to determine significant ($\alpha = 0.05$) pROC ratios >1.0 in the R package ENMGadgets (Barve & Barve, 2013). Second, Continuous Boyce Index (CBI, Hirzel *et al.* 2006) was used to measure how much environmental suitability predictions differ from a random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent with a Spearman correlation (r_s) with values ranging from -1 to +1. Positive values indicate predictions consistent with observed presences, with values close to zero no different than a random model. Negative values indicate areas with frequent presences having low environmental suitability. Mean CBI evaluation was calculated using five-fold cross-validation on 20% test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019).

Response curves, parameter estimates, percent contribution, permutation importance and a jack-knife test were used to measure variable performance within the best-fit model. Percent contribution is the relative increase to model gain that each variable makes to the optimal solution arrived at by MAXENT. This contribution is dependent on the particular algorithm path chosen. On the other hand, permutation importance is independent of the algorithm path and represents the importance of a given value on the AUC training values (Phillips *et al.* 2006). Jack-knife tests exclude each value, then develop the model with a sole variable to determine percentage contribution and regularized training gain

of each environmental variable to model performance. Training gain indicates how closely the model predicts the presence locations. The variables with the highest gain are those providing a good fit to the data and making greatest contribution to the final model. Whilst those variables decreasing the gain most when omitted are considered the most important explanatory variables (Phillips *et al.* 2006).

2.3.5 Reclassified binary prediction

To calculate potential range size, the continuous current prediction was reclassified to a binary (suitable/unsuitable) prediction to complement the current IUCN geographic range size. Currently there is no consensus on choosing binary thresholds and threshold selection can be an arbitrary process (Liu *et al.* 2013; 2016). Thus, a 10% training presence (10TP) was selected as a threshold that removes the lowest 10 % of predicted values accounting for any uncertainty in the occurrence data (Pearson *et al.* 2007), and visually best fitted current expert knowledge on harpy eagle distribution. The same 10TP threshold was used for the paleoclimate predictions because this provided a more realistic estimate for current range size to use for projecting into past climatic scenarios. Finally, Extent of Occurrence (EOO) was calculated with a minimum convex polygon around all occurrence points (excluding the ocean) following IUCN guidelines (IUCN 2019). General model development and spatial analysis were performed in R (v3.5.1; R Core Team, 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017), rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundle 2019) and sp (Bivand *et al.* 2013) packages.

2.3.6 Environmental ordination

To determine species-environment relationships in environmental space, the underlying environmental data at occurrence points were extracted using the three most important predictors from their contribution to model prediction. A random sample of 100,000 background points were extracted to represent the background environment, with occurrence data and environmental space defined using a minimum convex polygon. Ecological Niche Factor Analysis (ENFA, Hirzel *et al.* 2002; Basille *et al.* 2008) was calculated using all unfiltered occurrence points (n = 1179), against the background environmental data. ENFA directly measures environmental conditions at the presence points, thus spatial auto-correlation in occurrence data is not considered a serious issue (Basille *et al.* 2008). Including as many presence points as possible is therefore advisable in ENFA to obtain accurate measures of occupied environmental space (Hirzel *et al.* 2001).

ENFA is a multivariate, factorial analysis extracting two measures of the realized niche along two axes. The first axis metric, marginality (M), measures the position of the species ecological niche, and its departure relative to the available environment. A value of M >1 indicates that the niche deviates more relative to the reference environmental background and has specific environmental preferences compared to the available environment. The second axis metric, specialization (S), is an indication of niche breadth size relative to the environmental background, with a value of S >1 indicating higher niche specialization (narrower niche breadth). A high specialization value indicates a high reliance on the environmental conditions that mainly explain that specific dimension. ENFA was calculated in the R package CENFA (Rinnan 2018),

weighting all cells by the number of observations (Rinnan & Lawler 2019). Predictors were rescaled thus the ENFA can be interpreted similar to a PCA with eigenvalues and loadings represented along the first axis of marginality and the following secondary orthogonal axes of specialization (Basille *et al.* 2008).

2.4 Results

2.4.1 Species Distribution Models

The best-fit model ($\Delta AIC_c = 0.0$) had feature classes Linear and Quadratic with a regularization multiplier of $\beta = 1$. AUC metrics showed moderate predictive performance ($AUC_{TRAIN} = 0.698$, $AUC_{TEST} = 0.692$), with minimal overfitting ($AUC_{DIFF} = 0.06$) and high discrimination ability with omission rates close to expected values (MTP = 0.003, 10TP = 0.11). Testing the model against random expectations resulted in robust mean pROC ratios (pROC = 1.407, SD ± 0.057, range = 1.235-1.577), with high calibration accuracy between predicted environmental suitability and test occurrence points (Mean CBI = 0.838). The continuous best-fit model defined the spatial complexity in distribution for the harpy eagle, and identified an area of highest abiotic suitability across Amazonia (Fig. 2.1), with patchier distribution across southern Brazil and north into Central America (Fig. S2.3). Reclassifying the continuous prediction using the 10TP threshold (0.415; Fig. 2.2) gave an estimate for geographic range size of 9,844,399 km^2. Based on the occurrence data here EOO was estimated as 13,050,940 km^2.

In Brazil, the states of Amazonas and Pará had highest suitability, with further high suitability in Acre and Roraima states. Guyana had a large area of high environmental suitability, extending east into both northern Suriname and French Guiana, and west into southern Venezuela. In Bolivia and Peru, high suitability was identified along the entire east Andean slope, extending north into Ecuador. High suitability was identified across eastern Colombia despite only patchy occurrence records in the region. In Ecuador, high suitability was highlighted both along the Pacific slope and east of the Andes. In central

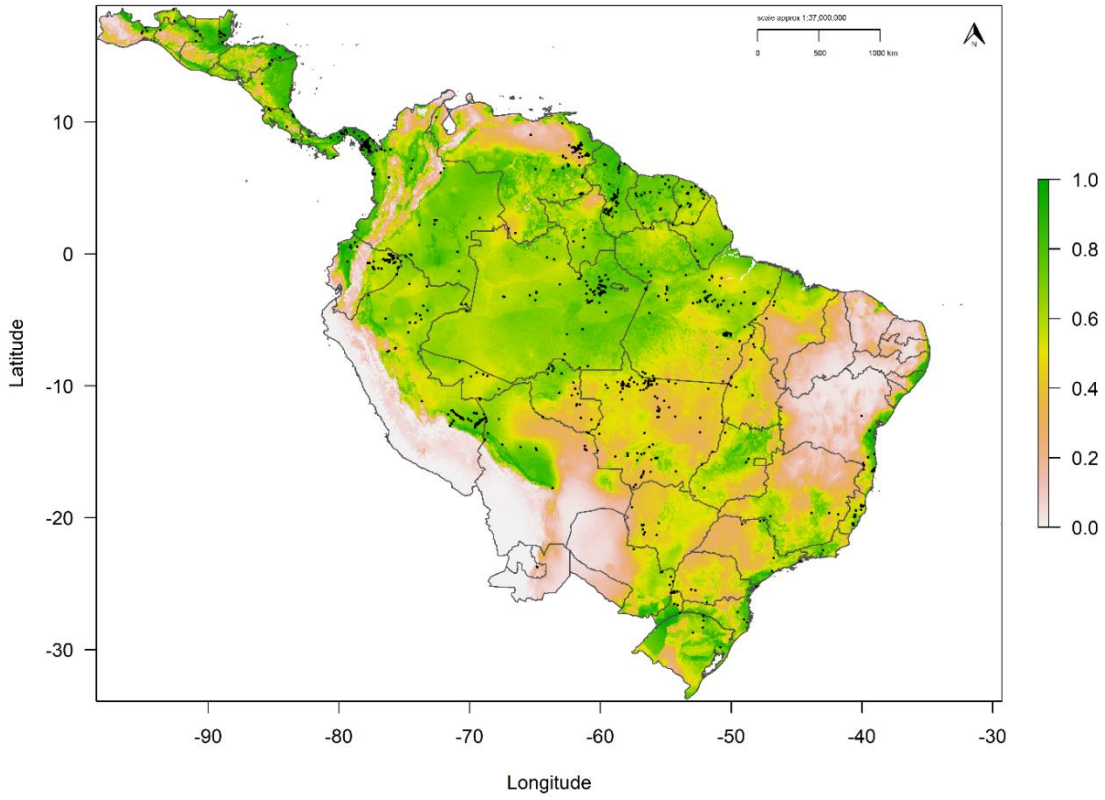


Figure 2.1. Predicted current distribution for the harpy eagle with values closer to 1 having highest environmental suitability. Grey lines define national borders and state boundaries for Argentina, Brazil, and Mexico. Black points define harpy eagle occurrences.

America, eastern Panama had very high environmental suitability, extending into west Panama, along the Carribbean Sea coast of Costa Rica, Nicaragua, eastern Honduras, and central-southern Belize (Fig. S3.3). Guatemala had disjunct high suitability, with a large area in the Peten Department conncected to central-southern Belize and a narrow strip along the Pacific coast (Fig. S3.3).

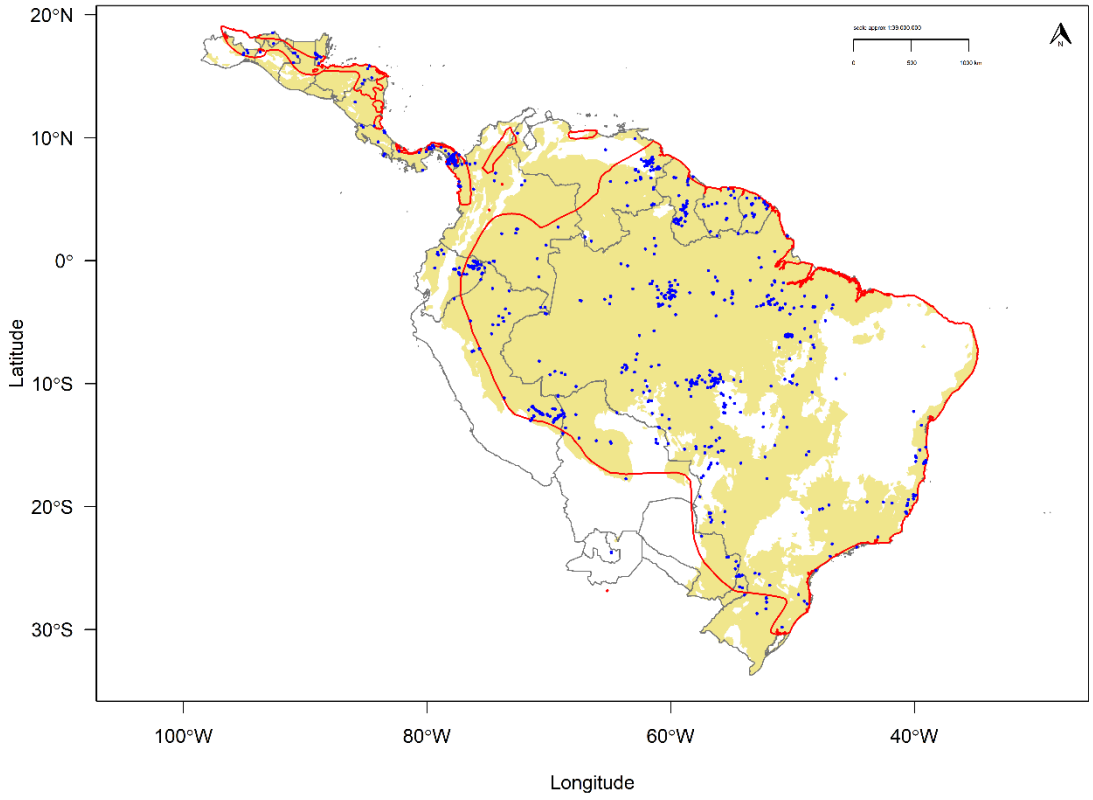


Figure 2.2. Reclassified binary range prediction using 10 % training presence (10TP = 0.415) threshold. Khaki area is the suitable environmental space above the 10TP threshold, white areas not suitable. Red polygons define current IUCN range for the harpy eagle. Grey lines define national borders and state boundaries for Argentina and Mexico. Blue points define harpy eagle occurrences.

2.4.2 Environmental predictors

From the parameter estimates, the harpy eagle was more likely to be associated with CMI and minimum temperature of the warmest month (Table 2.2). Overall, three predictors contributed 96 % to model prediction. Climatic Moisture Index (CMI) contributed the highest percentage (72.1 %, Table 2.3), with minimum temperature in the warmest month (15.6 %) and Terrain Roughness Index (TRI, 8.3 %) the next two highest contributions (Table 2.3). CMI had the highest regularized training gain, followed by precipitation in the

wettest month and minimum temperature in the warmest month (Fig. S3.4). CMI had the highest gain when used in isolation, so had the most useful information on suitable environmental conditions when used alone. CMI decreased the gain the most when omitted and could best explain the environmental requirements of the harpy eagle not present in the other predictors.

From the response curves there was a positive response to CMI peaking at ~0.4, with highest suitability for the minimum temperature of the warmest month increasing rapidly after 10 °C, peaking at 25 °C (Fig. 2.3). Precipitation in the wettest month peaked at 90mm/month, before levelling off up to 100 mm, with highest suitability for precipitation in the warmest quarter at 200 mm. Isothermality peaked at 9-10 %, reflecting the constant temperatures harpy eagles need in lowland tropical forests. PET in the driest quarter had highest suitability at 100 mm/month, but with highest suitability for PET in the wettest quarter at 50 mm/month indicating a preference for climates with greener vegetation. TRI peaked at 100 indicating high preference, as expected, for lowland flat areas with low terrain complexity.

Table 2.2. Parameter estimates derived from penalized logistic regression beta-coefficients fitted using Linear and Quadratic feature classes. Superscript 2 indicates only quadratic feature classes were needed to explain the response.

Predictor	Linear	Quadratic
Climatic Moisture Index	1.38	-3.62
Minimum temperature warmest month	0.13	
Maximum temperature warmest month	0.05	
PET driest quarter	0.03	0.00
Precipitation wettest month	0.02	
Terrain Roughness Index	0.02	0.00
Precipitation warmest quarter	0.00	
Isothermality[2]		-0.01
PET wettest quarter[2]		0.00

Table 2.3. Percent contribution and permutation importance for variables used as environmental predictors in the current distribution model for the harpy eagle. All values are %.

Predictor	Percent contribution	Permutation importance
Climatic Moisture Index[1]	72.1	43.1
Minimum temperature warmest month	15.6	22.8
Terrain Roughness Index[2]	8.3	12.4
PET driest quarter	3.0	9.8
PET wettest quarter	0.5	5.2
Isothermality[3]	0.2	5.2
Precipitation wettest month	0.2	5.2
Precipitation warmest quarter	0.0	0.7
Maximum temperature warmest month	0.0	0.4

[1] Ratio of annual precipitation to annual evapotranspiration
[2] Variation in local terrain around a central pixel
[3] Mean diurnal temperature range/temperature annual range*100.

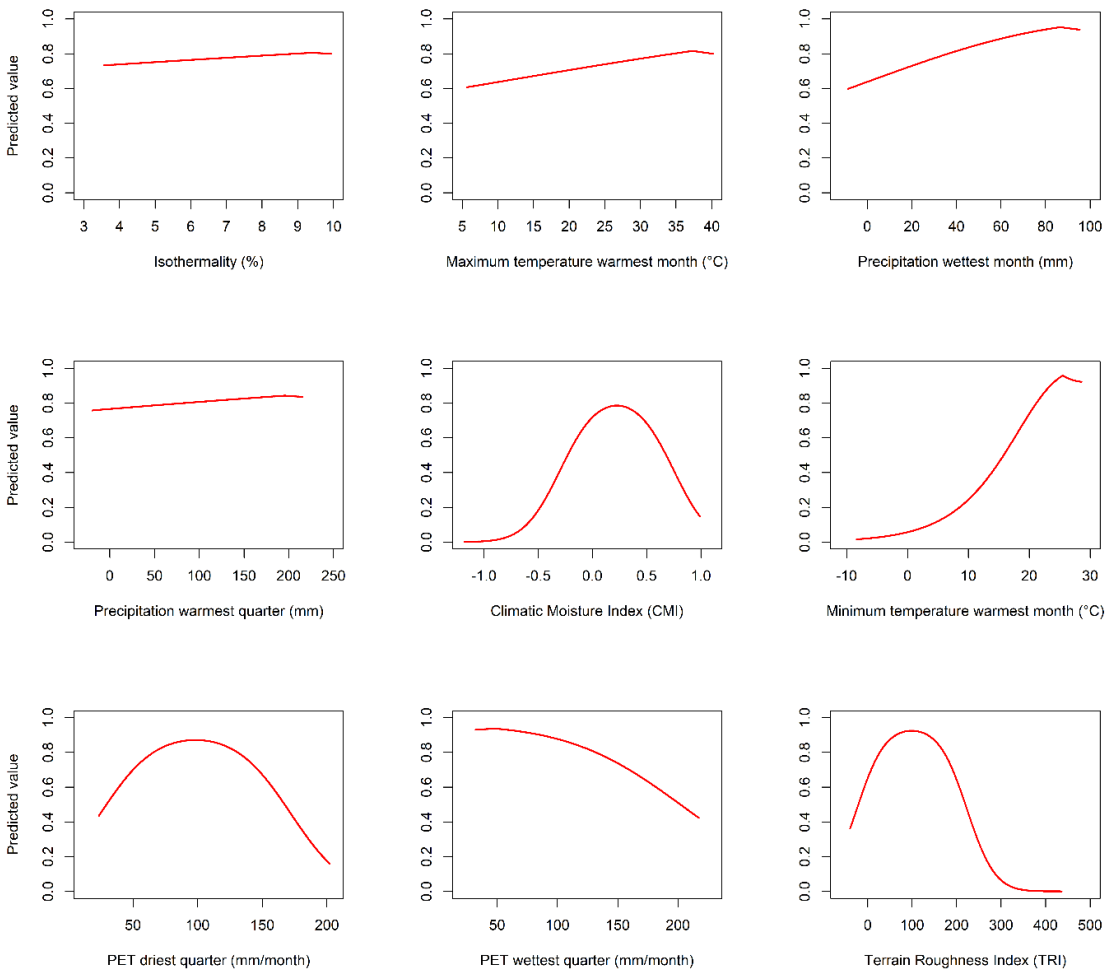


Figure 2.3. Response curves for climatic and topographical variables used as predictors in the current distribution model for the harpy eagle.

2.4.3 Environmental ordination

Within selected axes of environmental space harpy eagle occurrences were clustered within a Climatic Moisture Index ranging between -0.5 and 0.7 (Fig. 2.4a). Harpy eagle occurrences showed a lower limit for minimum temperature with no location points below 10.5 °C in the warmest month. Most occurrences were clustered around or above 20 °C (Fig. 2.4a), linked to the harpy eagle's preference for generally flat, lowland areas with low terrain complexity (Fig. 2.4b). Harpy eagle environmental space did not deviate substantially from the

average background environment available (Fig. 2.5), with the ENFA marginality factor slightly below the available background environment (*M* = 0.99). However, the harpy eagle is restricted to a particular environmental space relative to the reference environmental background with a narrow environmental niche breadth indicating highly specialized environmental requirements (*S* = 1.431). Five significant ENFA factors explained 80.75 % of the total variance in niche structure, with the first specialization axis (Spec1) explaining 28.81 % of this total (Table 2.4). CMI and precipitation in the wettest month were the two highest coefficients on the marginality axis, with minimum temperature in the warmest month the highest on the specialization axis.

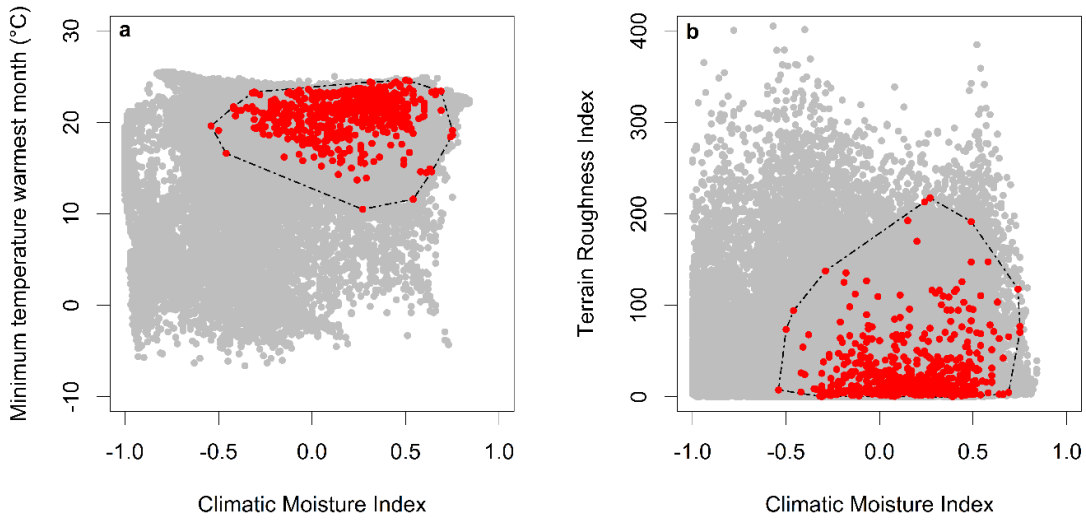


Figure 2.4. Distribution of harpy eagle occurrences in selected pairs of environmental variables. Grey points are random background environmental points, red points are harpy eagle occurrences. Black hashed line defines the minimum convex polygon of harpy eagle occurrences.

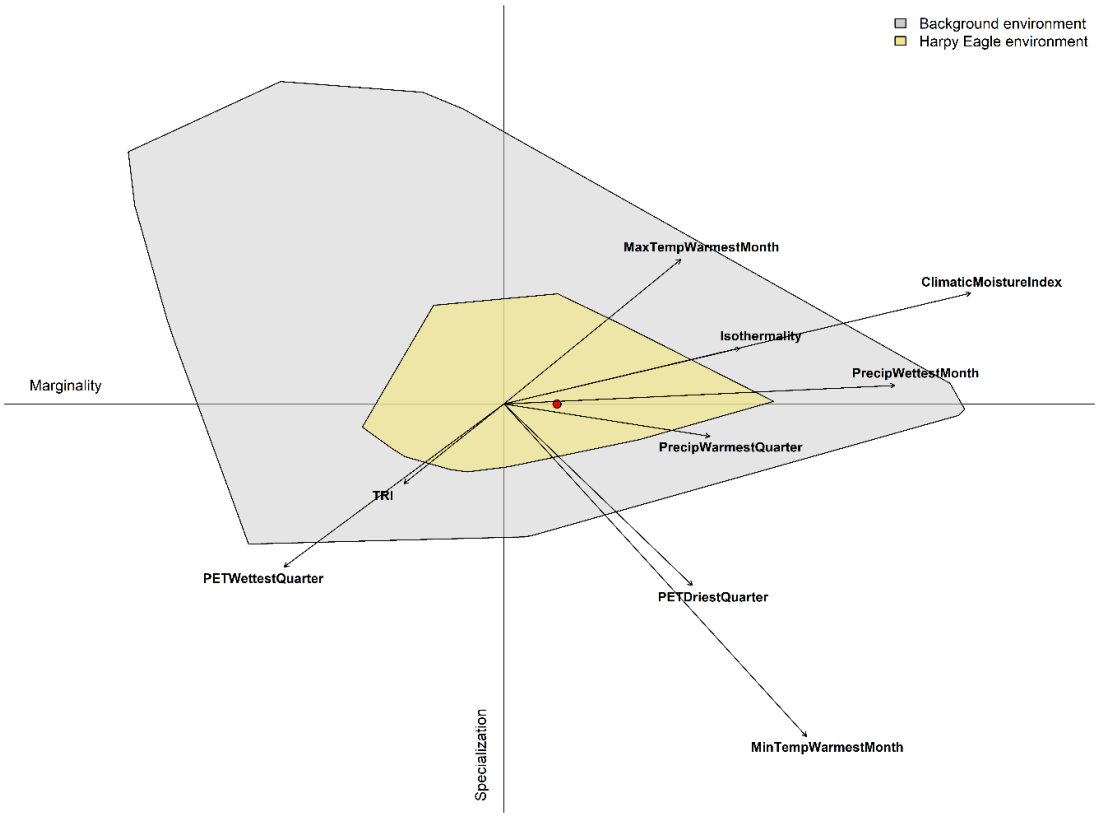


Figure 2.5. Ecological Niche Factor Analysis (ENFA) for suitable harpy eagle environment space (khaki) within the available background environment (grey) shown across the marginality (x) and specialization (y) axes. Arrow length indicates the magnitude with which each variable accounts for the variance on each of the two axes. Red circle indicates niche position (median marginality) relative to the average background environment (the plot origin).

Table 2.4. Variance explained by the five most significant ENFA factors (Marg. = marginality; Spec = Specialization). Coefficient values for the nine environmental predictors are ordered according to the highest coefficient values in the marginality factor.

ENFA axis	Marg	Spec1	Spec2	Spec3	Spec4
Variance explained (%)	14.05	28.81	13.82	12.51	11.56
Predictor					
Climatic Moisture Index	0.56	0.24	-0.08	-0.24	0.26
Precipitation wettest month	0.47	0.04	0.00	-0.05	-0.04
Min. temp. warmest month	0.36	-0.72	-0.30	-0.28	-0.27
Isothermality	0.28	0.12	0.03	0.08	0.33
PET wettest quarter	-0.26	-0.35	-0.31	-0.40	0.20
Precipitation warmest quarter	0.25	-0.07	0.01	0.15	-0.15
PET driest quarter	0.23	-0.39	-0.49	-0.19	-0.56
Max. temp. warmest month	0.21	0.31	0.73	0.77	0.57
Terrain Roughness Index	-0.12	-0.17	-0.18	0.23	0.21

2.4.4 Paleo-distributions

All individual paleoclimate GCMs predicted similar paleo-distributions with high geographical niche overlap (Table S2.1, Figs. S2.5-S2.6). From the mean projections, hindcasting the current prediction to the LGM defined a large area of high suitability across northern-central South America. A further strip of high suitability extended from present-day Panama, south along the Pacific slope west of the Andes into the present-day Chocó region of Colombia and west Ecuador (Fig. S2.7, top left). In the Mid-Holocene high suitability areas increased, extending north into Central America, across Amazonia and east in present-day Brazil (Fig. S2.7, top right). During the LGM mean range size was 17 % smaller (Fig. S2.7, bottom left; Table S2.2), compared to the current 10TP geographic range size (9,844,399 km^2). In the Mid-Holocene, range size had increased from the LGM, but was still 6 % smaller than the current 10TP range

size estimate (Table S2.2, Fig. S3.7, bottom right). Areas of highest stable climate refugia were identifed in the central Amazon basin north into Guyana, south-east Colombia and Panama (Fig. 2.6), consistent with these areas having continuous high suitability since the LGM.

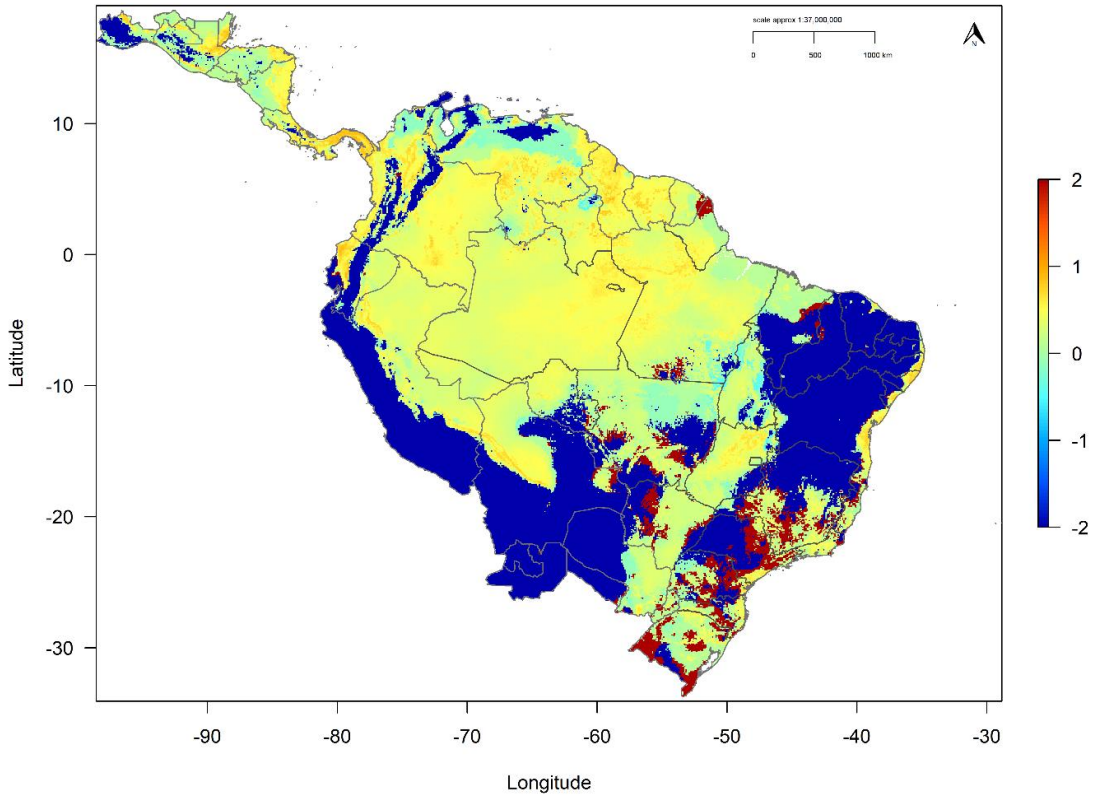


Figure 2.6. Predicted climate stability for the harpy eagle summed from the current, Last Glacial Maximum (LGM, ~22,000 years ago) and Mid-Holocene (~6,000 years ago) predictions. Values of -2 indicate species absence, -1 to 0 shows colonizable areas, 0 to 1 defines areas of highest stability and values of 2 (dark red patches) show the most unstable areas. Map defines summed prediction masked to current geographic extent and geo-political boundaries.

2.5 Discussion

More than half of all global raptor species have declining populations, and there are significant knowledge gaps on the extent of their distribution and ecological requirements (McClure *et al.* 2018). In particular, accurate distribution estimates are lacking for many tropical forest raptors (Sarasola *et al.* 2018; Buechley *et al.* 2019). Here, I provide an analytical framework for applying predictive spatial models to address these fundamental issues to a tropical forest raptor. More broadly, I propose this analytical framework as an efficient and cost-effective approach to tackling this problem across all taxa. Using a PPM regression framework is now viewed as one of the most effective methods to determine species distributions and relative abundance (Aarts *et al.* 2012; Renner *et al.* 2015; Isaac *et al.* 2019), as supported by the results here. Using climatic and topographical predictors resulted in high model predictive performance, defining in more detail the spatial and environmental requirements for the harpy eagle across its geographical range. However, it is recognised that including predictors such as landcover and human impact, which are changing rapidly, would improve predictions. These, however, will be analysed and presented elsewhere.

2.5.1 Spatial requirements

How species are distributed in geographical and environmental space is fundamental to conservation planning (Loiselle *et al.* 2003; Pearce & Boyce 2006). Yet accurate and reliable spatial information, such as geographic range size and environmental constraints, are often lacking in many tropical biodiversity assessments (Cayuela *et al.* 2009; Tobias *et al.* 2013), and specifically for Neotropical raptors (Sarasola *et al.* 2018). Using a PPM

framework enables the predictions given here to be interpreted as areas of relative abundance (Renner *et al.* 2015; Phillips *et al.* 2017) under the assumption that historical habitat is still intact. Building on a previous SDM (Miranda *et al.* 2019), our continuous prediction adds further spatial detail showing a discontinuous distribution. This is likely a consequence of patchy environments, resulting in spatial heterogeneity in harpy eagle distribution. Miranda *et al.* (2019) used both climatic and vegetation predictors, and there is a close visual correspondence between their predictions and both the continuous and binary models here. This suggests that at the continental scale biologically relevant climatic and topographical predictors alone can accurately predict the distribution for the harpy eagle.

The models here refine previous coarse estimates of harpy eagle distribution (Ferguson-Lees & Christie 2005; Birdlife International 2017), providing an empirically derived range size to complement the species' current IUCN status. The binary threshold estimate of geographic range size (Fig. 2; 9,844,399 km^2), was 11 % smaller than the current IUCN polygon (11,064,295 km^2), and the estimated EOO (13,050,940 km^2) was 25.9 % less than the current IUCN EOO (17,600,000 km^2). Based on these figures I recommend reviewing the IUCN distributional area for the harpy eagle, which can over-estimate avian geographic range sizes (Jetz *et al.* 2008; Peterson *et al.* 2016; Ramesh *et al.* 2017). Specifically, the removal of semi-arid areas (such as the Caatinga in eastern Brazil) from across the IUCN range would show a more realistic geographic distribution. The Caatinga area had low predicted suitability, no current or historical occurrence records, and was not predicted suitable for the harpy eagle including during the last glacial maximum (LGM). Similarly, the

Cerrado (in central Brazil) was not predicted as suitable for the harpy eagle either during the LGM, and all recent records for the species show no evidence of breeding in the area. Although early naturalists reported breeding harpy eagles in this region (Sick & Barruel 1984), there is no evidence of a functional population and the area should be removed from the IUCN range polygon (and any present range projections) following IUCN guidelines for not including areas where the species does not exist (IUCN 2019).

2.5.2 Species-Environment relationships

The continuous model highlighted distinct areas of high environmental suitability (Fig. 2.1), with the binary model closely matching the primary vegetation types for recognized harpy eagle habitat (lowland tropical broadleaf forest, Beck *et al.* 2018). Thus, in the Chocó biogeographic region of north-west Ecuador and south-west Colombia west of the Andes, the current model defined areas of high environmental suitability, which correlate with new records of harpy eagles in the Pacific slope region (Muñiz-López 2005; Muñiz-López *et al.* 2007; Zuluaga *et al.* 2018). However, due to continued habitat loss in this area and across the species range, climatically suitable areas predicted for some regions may over-represent suitability where there is no longer harpy eagle forest habitat. The models here also defined previously unrecognized areas of high environmental suitability in south-east Colombia, northern Guyana, and along the east Andean slope of Peru and Bolivia. All these regions may hold viable populations of harpy eagles, with further research and continued surveys in these areas recommended where possible.

Environmental suitability predicted for the harpy eagle largely correlates with habitat selection studies from Amazonian Peru (Robinson 1994). Here, highest frequency of harpy eagle sightings were recorded in mature flood plain forest, with high nesting densities below 300 m elevation in lowland humid forest in Darien, Panama (Vargas González & Vargas 2011), analogous to the environmental suitability predictions here. Due to the rarity and large home range sizes of harpy eagles, Thiollay (1989) was not able to provide population density estimates from French Guiana, but suggested harpy eagles are rare but widespread throughout the largely tropical lowland forest in the region, consistent with the results here. Although largely thought to be extirpated from much of Central America, the models here identify areas of high suitability for harpy eagles along the Caribbean slopes of Costa Rica, Honduras, Nicaragua and Panama (Fig. S2.3), which should be prioritised for continued surveys and habitat protection.

Using the combined analytical approach enabled a further development of the spatial modelling process by unravelling the preferred environmental space and ecological conditions where harpy eagle abundance should be at its highest (VanDerWal *et al.* 2009; Osorio-Olvera *et al.* 2019). Climatic Moisture Index (CMI) was the most important environmental variable defining harpy eagle distribution, with a preferred CMI = ~ 0.4 (Fig. 2.3), along with the highest model gain when used solely in a jack-knife test, demonstrating its importance to account for harpy eagle distribution. This indicates a preference for wet, moist environments, correlating with lowland tropical forest across Central and South America (Willmott & Feddema 1992; Beck *et al.* 2018), and suggests that CMI may be a useful surrogate predictor for habitat in tropical areas. Aligned with

CMI and lowland tropical forest distribution was the positive response to higher minimum temperatures in the warmest month (Fig. 2.3). Harpy eagle environmental suitability was highest in areas with a minimum temperature of ~24 °C, reflected in the stable temperature conditions found across lowland tropical forests.

Assessing harpy eagle distribution in environmental space revealed similar patterns of environmental tolerances to the geographical models (Figs. 2.4-2.5), with CMI having the highest positive correlation with harpy eagle occurrence. However, precipitation in the wettest month was also highly correlated with harpy eagle occurrence (Table 2.4), following the general observation for tropical regions that seasonal rainfall patterns are the main limiting factor for primary productivity and therefore species distributions (Schloss *et al.* 1999; Williams & Middleton 2008). The ENFA confirmed the specialized environmental requirements for the harpy eagle, strongly linked to CMI and precipitation, which are likely operating as useful surrogate predictors of lowland tropical forest habitat. Importantly, minimum temperature of the warmest month (MTWM) had a high negative coefficient value on the specialization axis (Table 2.4). This indicates that MTWM is a key climatic predictor restricting harpy eagle distribution, linked to harpy eagle preference for lower elevations (Piana 2007; Muñiz-López 2008; Vargas González & Vargas 2011). Harpy eagle nests are rarely found above an altitude of 300m (Vargas González & Vargas 2011), and as temperature and elevation are closely correlated it seems likely the harpy eagle is negatively responding to lower temperatures at higher elevations restricting breeding distribution.

2.5.3 Paleo-distributions

The two paleoclimate predictions given here place current harpy eagle distribution in context. During the LGM, highest suitability was centred on northern and western Amazonia and present-day Panama (Fig. S2.7, top left). This follows current evidence that suggests during the LGM much of Amazonia was forested (Mayle *et al.* 2004), contrary to the rainforest refugia hypothesis (Haffer 1969). However, forest structure was likely quite different from the present-day, due to lower temperatures, rainfall and atmospheric CO_2 (Mayle *et al.* 2004), resulting in mixed-forest communities. Climate reconstructions from Amazonia during the LGM show that temperatures were 5 °C cooler than today (Guilderson *et al.* 1994; Stute *et al.* 1995), and that rainfall was spatially highly variable, as it is in the present-day. Thus, dry forest-savannahs may have dominated the region of central and southern Amazonia during the LGM, which may explain the low environmental suitability for the harpy eagle in this region from the LGM paleo-climate model.

During the Mid-Holocene the continuous prediction was similar to the current model with expansion of high suitability across Amazonia and north into Central America (Fig. S2.7, top right). This may be explained by the correlation of these areas with expansion of deciduous broadleaf forest in the region during the Mid-Holocene, ultimately related to changing precipitation levels (Mayle *et al.* 2004). The increase in distributional area size during this period correlates with a population expansion identified from genetics from 60,000 cal yr BP, well before the LGM, and subsequently through the Mid-Holocene (Lerner *et al.* 2009). The population expansion prior to the LGM occurred with climatic changes in Amazonia, leading to a reduction of tropical forest (Mayle *et al.* 2004), followed

by expansion of forest through the LGM and Mid-Holocene up to pre-Industrial times. Thus, harpy eagle distribution area is strongly associated with changing climatic conditions (and therefore vegetation), which suggests a potential reduction in range size under future drier climate change conditions predicted across much of Central and South America (da Costa *et al.* 2010). However, our stable refugia prediction identified key areas of stable conditions since the LGM where a suitable climatic envelope for the harpy eagle is likely to persist into the future (Fig. 2.6). We recommend these areas be prioritized for conservation and research, holding some encouragement for the future survival of the species as long as habitat can be maintained.

2.5.4 Conclusion

Explaining the observed distribution and ecological constraints of an organism by reference to its environmental requirements is one of the central goals in ecology (Krebs 2009). Species at high trophic levels with slow life histories are often at increased risk of extinction (Purvis *et al.* 2000). Therefore, understanding the environmental processes regulating distribution of apex predators is an especially pressing conservation need. By refining previous range estimates using relevant abiotic variables (including those that may act as vegetation surrogates), the models here define the ecological processes shaping both current and past harpy eagle distribution. Subsequent distribution models should include variables such as biotic interactions, landcover and human impacts at broad and fine scales to improve current predictions, and project into future climate change scenarios. With recent work demonstrating strong relationships between suitability predictions from SDMs and species abundance (Weber *et al.* 2017, Osorio-Olvera *et al.* 2020), I confirmed the

suitability of spatial point process models to deliver cost-effective and reliable first estimates of relative species abundance for conservation management. Having accurate distributional data on the current ranges of tropical birds and raptors has long been a priority in the Neotropics (Snow 1985; Bierregaard 1998). Using a range of spatial modelling methods, I was able to establish a baseline of ecological constraints for the harpy eagle that may help to better plan its conservation across its vast continental distribution.

2.6 Appendices

Appendix 1 Supplementary Tables

Table S2.1. Geographical niche overlap calculated for predicted paleo-distributions for the harpy eagle at the Last Glacial Maximum (~22,000ya) and Mid-Holocene (~6,000ya) using three paleoclimate General Circulation Models (GCMs).

Last Glacial Maximum

GCM	CCSM4	MIROC-ESM
MIROC-ESM	0.836	
MPI-ESM-P	0.841	0.814

Mid-Holocene

GCM	CCSM4	MIROC-ESM
MIROC-ESM	0.871	
MPI-ESM-P	0.896	0.869

Table S2.2. Geographic range size estimates from predicted paleo-distributions for the harpy eagle at the Last Glacial Maximum (~22,000ya) and Mid-Holocene (~6,000ya) using three paleoclimate General Circulation Models (GCMs). Area difference for each Paleoclimate GCM is compared to the reclassified 10TP current threshold prediction.

Paleoclimate scenario	GCM	Area (km^2)	Area difference (km^2)	%
Last Glacial Maximum	CCSM4	7,040,774	2,803,625	-28.48
	MIROC-ESM	9,422,859	421,540	-4.28
	MPI-ESM-P	7,914,406	1,929,993	-19.60
	Mean	8,126,013	1,139,386	-17.45
Mid-Holocene	CCSM4	9,292,721	551,678	- 5.60
	MIROC-ESM	9,436,390	408,009	-4.14
	MPI-ESM-P	9,013,362	831,037	-8.44
	Mean	9,247,491	596,908	-6.06

Appendix 2 Supplementary Figures

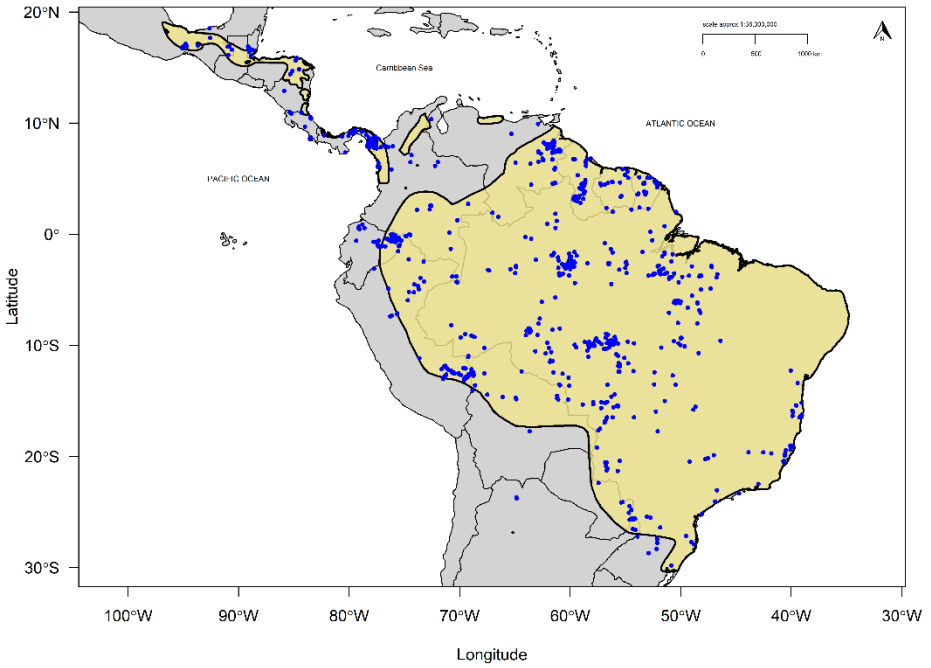


Figure S2.1. Current IUCN range map for the harpy eagle overlaid with unfiltered harpy eagle occurrence data (blue points) used in this study.

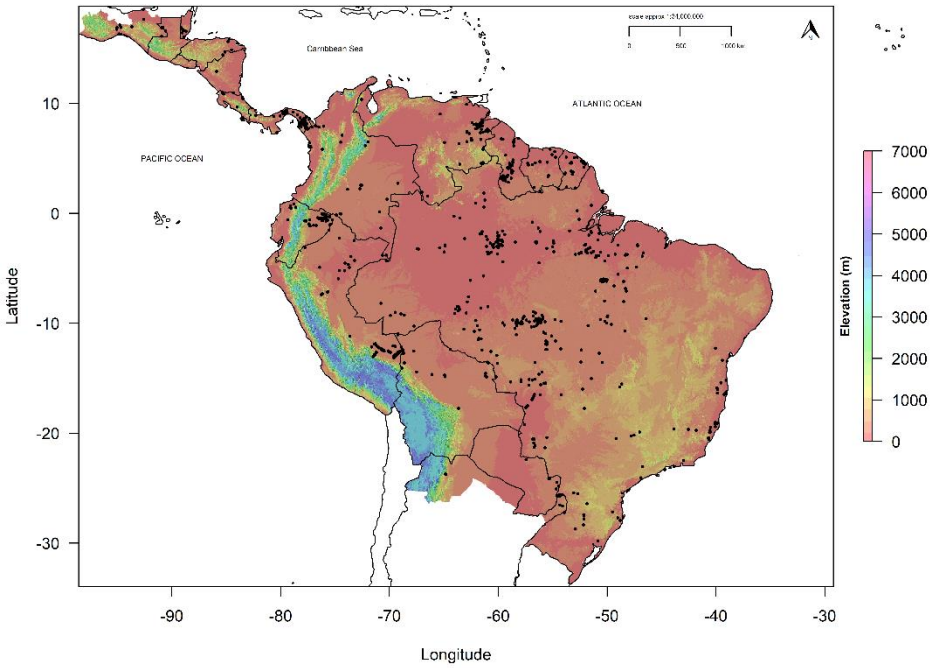


Figure S2.2. Digital Elevation Model showing distribution of harpy eagle occurrence data (black points) used in this study after applying a 4km spatial filter on the raw occurrence points.

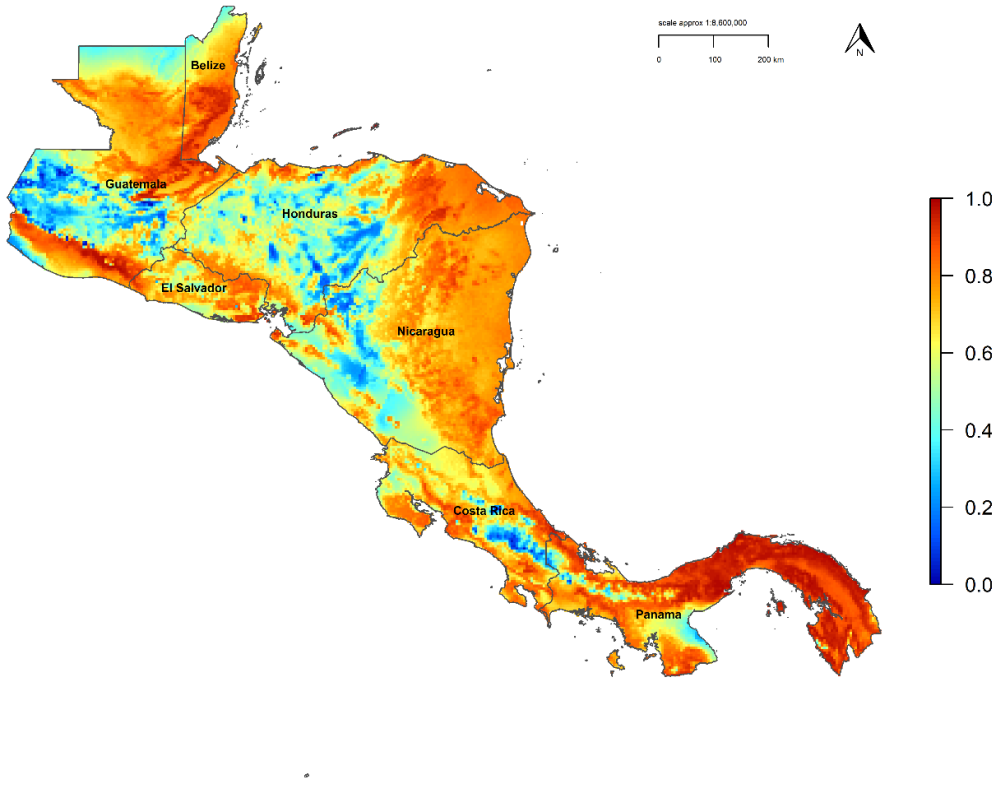


Figure S2.3. Projected distribution model for the harpy eagle for Central America. Map denotes complementary log log (cloglog) prediction with values closer to 1 defining higher environmental suitability for harpy eagle occurrence.

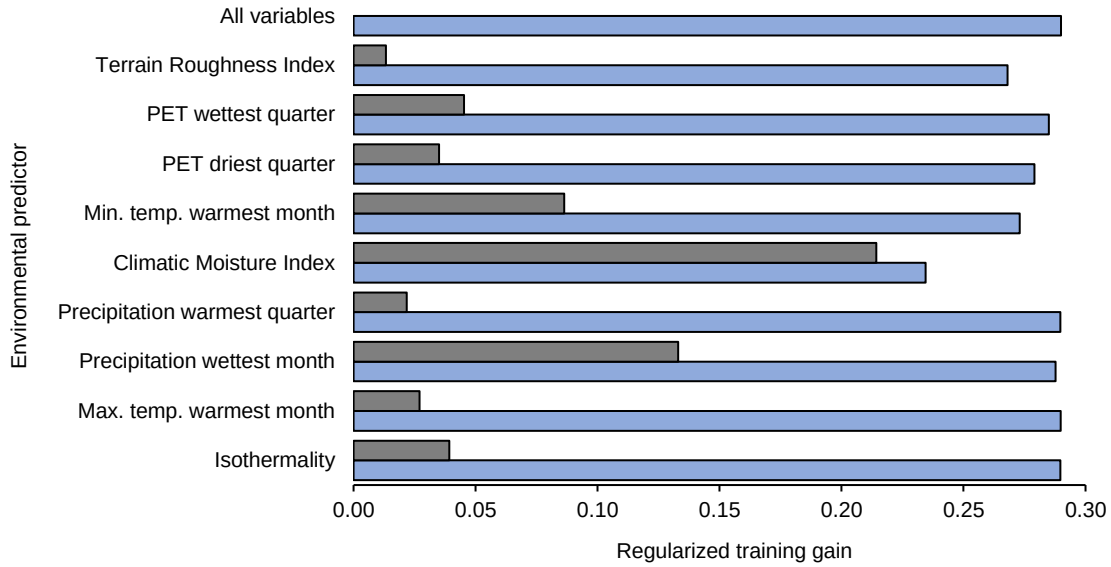


Figure S2.4. Variation in regularized training gain for climatic and topographical predictors using a jack-knife test of variable importance. Blue bars represent regularized gain without the variable and dark grey bars represent regularized gain with only the one variable.

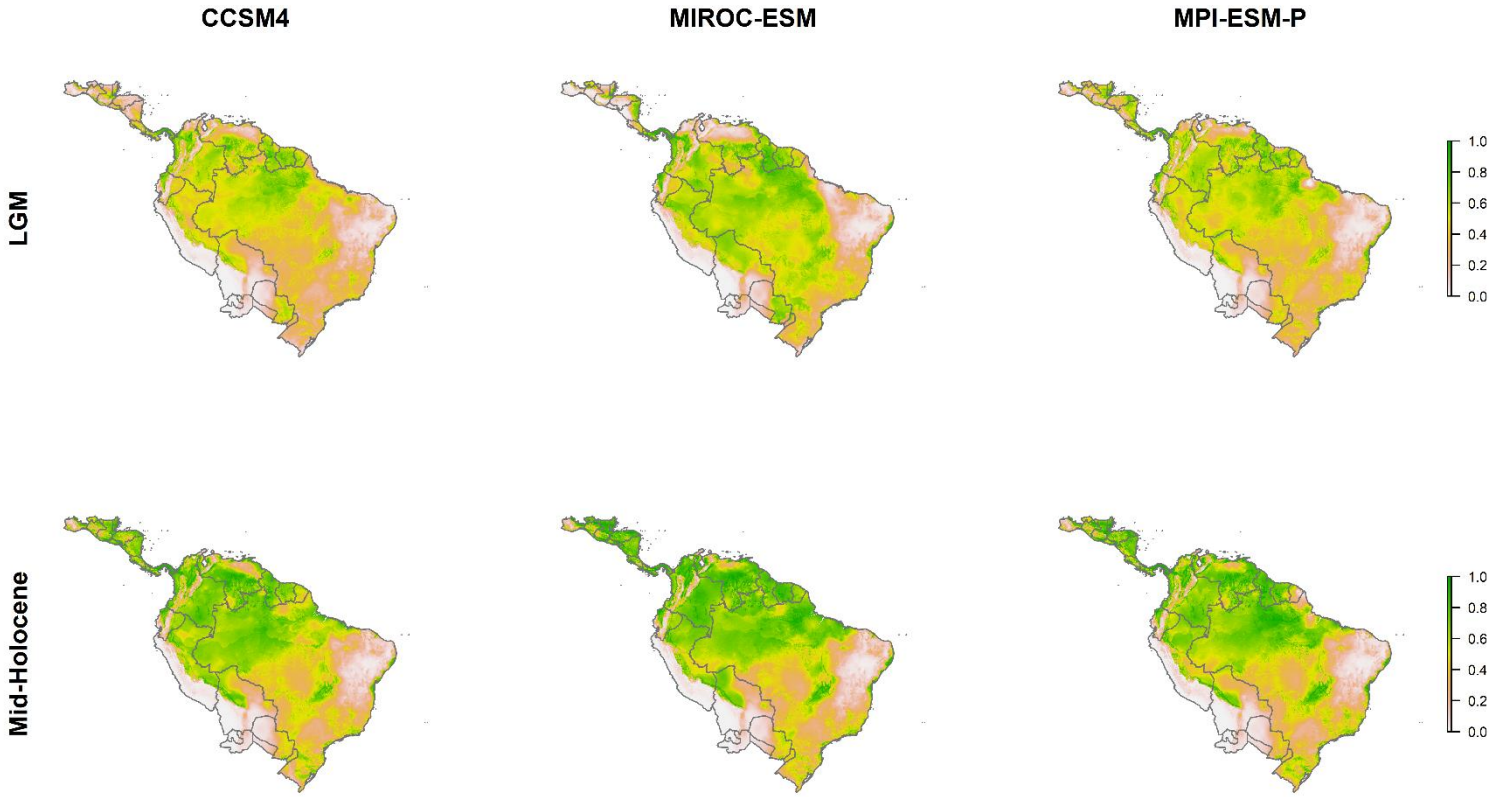


Figure S2.5. Predicted continuous Paleo-distributions for the harpy eagle projected to the Last Glacial Maximum (LGM, ~22,000ya) and Mid-Holocene (~6,000ya) across three paleoclimate General Circulation Models (GCMs). Maps denote complementary log-log (cloglog) prediction with values closer to 1 defining higher environmental suitability for harpy eagle occurrence.

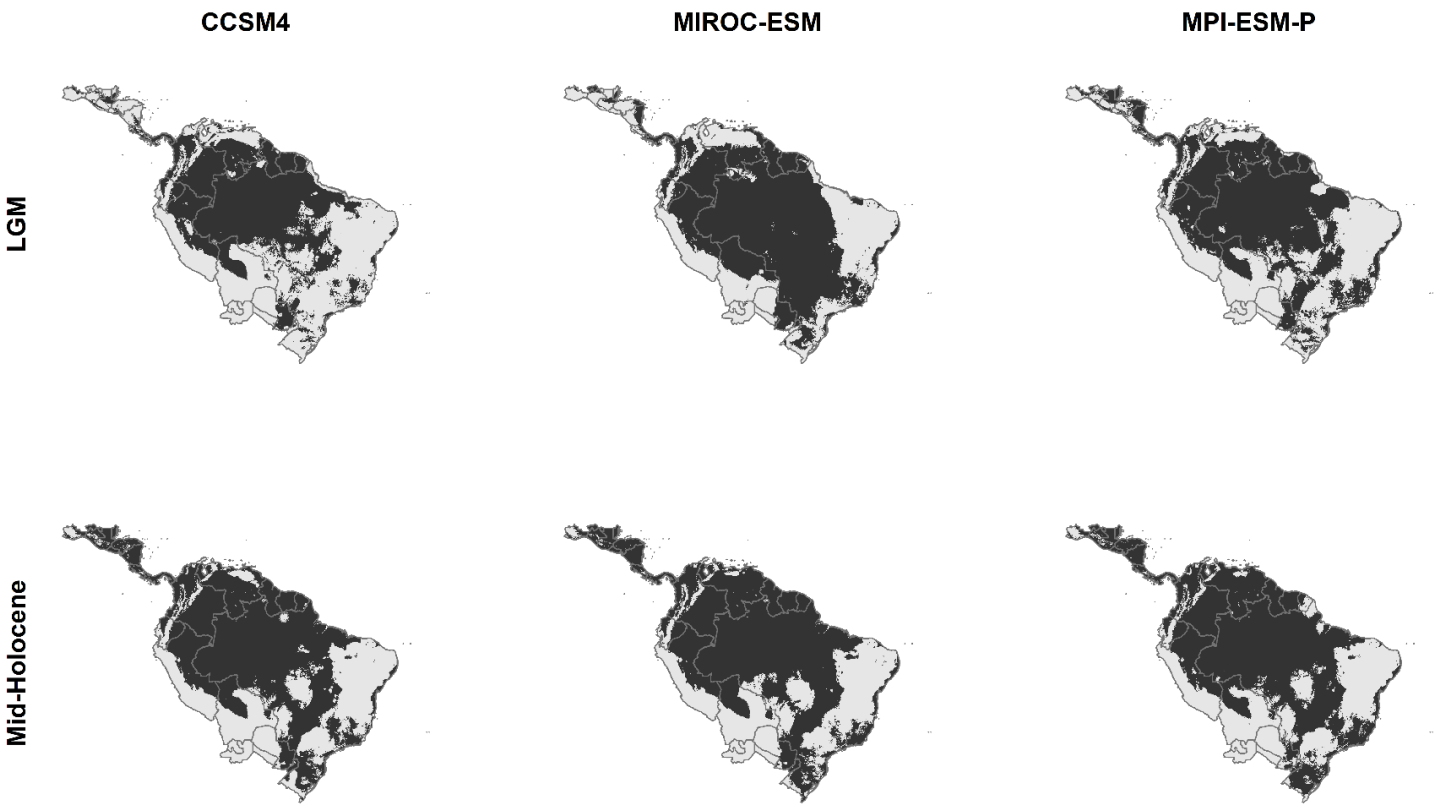


Figure S2.6. Predicted Paleo-distributions for the harpy eagle projected to the Last Glacial Maximum (LGM, ~22,000ya) and Mid-Holocene (~6,000ya) reclassified to binary predictions across three paleoclimate General Circulation Models (GCMs). Black areas are suitable environmental space above the 10TP threshold (0.415).

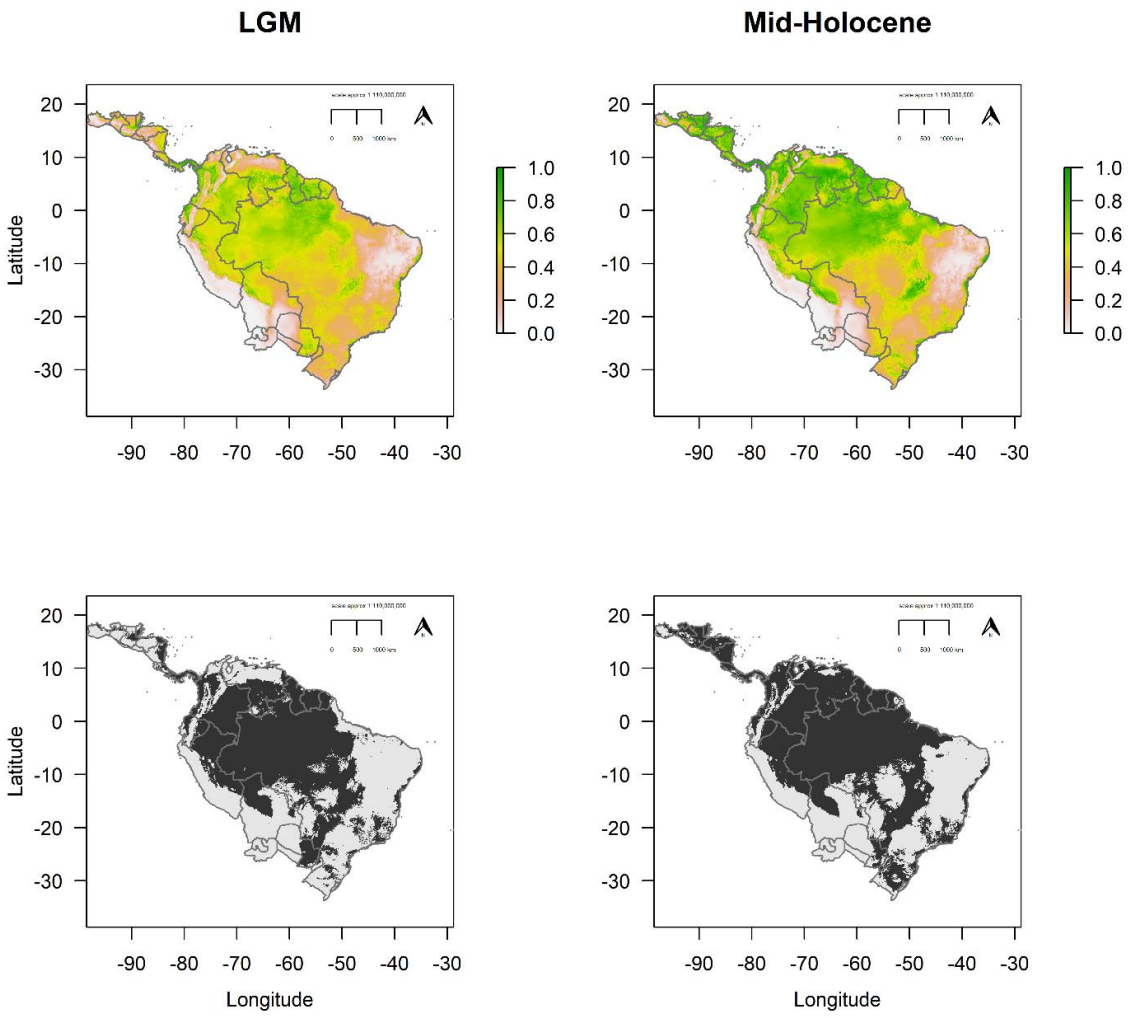


Figure S2.7. Predicted paleo-distributions for the harpy eagle projected to the Last Glacial Maximum (LGM, ~22,000 years ago) and Mid-Holocene (~6,000 years ago). Maps define the mean predictions from the three paleoclimate General Circulation Models masked to current geographic extent and geo-political boundaries.

3. Prey resources are more important than abiotic conditions for predicting the distribution of a broad-ranged apex predator.

3.1 Abstract

A current biogeographic paradigm states that climate regulates species distributions at continental scales and that biotic interactions are undetectable at coarse-grain extents. However, recent advances in spatial modelling show that incorporating food resource distributions are important for improving model predictions at large distribution scales. This is particularly relevant to understand the factors limiting distribution of widespread apex predators whose diet is likely to vary across its range. The harpy eagle (*Harpia harpyja*) is a large Neotropical raptor, whose diet is largely comprised of arboreal mammals, such as sloths and primates, all with broad distributions across Neotropical lowland forest. Here, I use a hierarchical modelling approach to quantify the relative importance of abiotic factors and food resource distribution that predict the range limits for the harpy eagle. This hierarchical approach consisted of the following modelling sequence of explanatory variables: (a) abiotic predictors only, (b) the food resource distributions predicted by an equivalent modelling for each prey, (c) the combination of abiotic factors and food resources (i.e., a+b), and (d) as in (c) but with food resources considered as a single, summed prediction equivalent to prey species richness. Incorporating prey distributions improved model predictions but using solely these biotic predictors still resulted in a high performing model. In the Abiotic model, Climatic Moisture Index (CMI) was the most important predictor, contributing 80 % to model prediction. Three-toed sloth (*Bradypus* spp.) was the most important resource predictor, contributing 57.1 % in a combined Abiotic-Biotic model, followed by CMI

contributing 28.6 %. Harpy eagle distribution had moderate to high environmental overlap across all prey distributions in geographic space when measured individually, but this overlap was substantially lower in environmental space when prey distributions were combined. With strong reliance on prey distributions across its range, harpy eagle conservation programs must therefore consider its most important food resources as a key element in the protection of this threatened raptor.

3.2 Introduction

In biogeographic theory, climate is hypothesised to be the main driver of species distributions at continental scales (Pearson & Dawson 2003; Wiens 2011; Louthan *et al.* 2015). This is evidenced through the fossil record (Davis & Shaw 2001), and recent observed trends (Walther *et al.* 2002; Parmesan & Yohe 2003). However, the relationship between distribution and climate may be either indirect (Rich & Currie 2018), an oversimplification (Dallas *et al.* 2017), or due to historical biogeography (Heads 2015). Yet, whether biotic resources are more important determinants of species distributions than climatic conditions is still an unresolved question in ecology and biogeography (Andrewartha & Birch 1954; MacArthur 1972; Wisz *et al.* 2013; Araújo & Rozenfeld 2014; Heads 2015; King *et al.* 2020). The current paradigm postulates that biotic resources are most apparent at finer geographical scales (Pearson & Dawson 2003; Peterson *et al.* 2011), but this assertion may not apply across all taxa.

Biotic effects may be lost at continental scales due to the coarse-grain extent, commonly termed the Eltonian Noise Hypothesis (ENH, Soberón & Nakamura 2009). The ENH postulates that because biotic interactions occur at a fine-scale

individual level, modelling approaches will fail to recognize them when working at coarse continental scales. Alternatively, biotic resources may correlate closely with abiotic factors, thus the biotic signal is lost in abiotic environmental space (Brewer & Gaston 2003). The effect of biotic resources on species distributions can vary markedly across a given species geographic range (Thompson 2005). Even so, the overriding assumption is that biotic resources require a fine-scale spatial structure to be noticeable (Soberón & Nakamura 2009) because by definition biotic interactions occur at the individual level (Anderson 2016). This assumption is applied to multiple biotic interactions such as the presence or absence of mutualists, competitors, and predators. In a marine environment, including food resource distributions in spatial models for sea kraits (genus: *Laticauda*) improved distribution predictions (Ghergel *et al.* 2018). However, the possible influence of prey species distributions on the continental distribution of a terrestrial apex predator has so far not been investigated.

The relationship between the range limits of animals, such as butterflies and nectivorous birds being driven by the distribution of their food plants, is well established (Wisz *et al.* 2013; Kass *et al.* 2019). However, it is still unclear if the same processes act on the distribution of large vertebrate apex predators which are dependent on a variety of vertebrate food sources (Sih 2005; With 2019). It is well-known that apex predators can limit the distribution of their prey species (Holt & Barfield 2009). However, an outstanding question for large vertebrates is whether the distribution of food resources limits the distribution of their main consumers (Sih 2005; Aragón & Sánchez-Fernández 2013; Louthan *et al.* 2015; Schweiger *et al.* 2015). The expectation would be for a high overlap between

the abiotic conditions in the predator's distribution and those of its prey. Consumer (i.e., predator) distribution should be nested within their main resource distributions (Holt 1997), but conversely food resource distributions are not reliant on the distribution of their main consumers.

Food resource distributions can be an important predictor for estimating avian distributions at regional or landscape scales (Aragón & Sánchez-Fernández 2013; de Araújo *et al.* 2014; Aragón *et al.* 2018). However, whether the distribution of food resources can successfully predict the presence of a main consumer across continental extents (2000 – 10,000 km) has not been tested specifically for a terrestrial apex predator. The harpy eagle (*Harpia harpyja*) is a large Neotropical raptor with a continental range across Central and South America from southern Mexico to northern Argentina (Ferguson-Lees & Christie 2005; Vargas González *et al.* 2006). Harpy eagles are distributed across lowland tropical forest (Vargas González & Vargas 2011; Miranda *et al.* 2019; Sutton *et al.* 2021), and in seasonal forest enclaves (Silva *et al.* 2013). A recent review summarizing harpy eagle diet across its range established a trend towards a semi-specialized diet (Miranda 2015), mainly comprised of arboreal mammals, including sloths, primates, and tree porcupines. However, birds, reptiles, and terrestrial mammals may also be taken, albeit less frequently (Aguiar-Silva *et al.* 2015; Miranda 2018; Miranda *et al.* 2020).

Species Distribution Models (SDMs) are spatial statistical models that establish the environmental distribution of a given species from environmental conditions at known occurrences (Franklin 2009; Peterson *et al.* 2011). SDMs have seen rapid advances over the past 20 years, yet there are still outstanding conceptual

and methodical issues that need addressing to improve predictions (Guisan *et al.* 2017). An important current ecological question is whether including biotic interactions in SDMs can increase their predictive power (Wiens 2011; Wisz *et al.* 2013; Anderson 2016; Dormann *et al.* 2018). Incorporating food resource distributions into abiotic SDMs can improve model predictive performance, leading to more realistic predictions at regional scales (Aragón *et al.* 2018; Atauchi *et al.* 2018*;* Palacio & Girini 2018). Moreover, including biotic resources in SDMs is especially relevant for species ranging over lower tropical latitudes with more benign abiotic conditions (Louthan *et al.* 2015). Indeed, it has long been hypothesised that species range limits in low-latitude areas are driven more by species interactions than climate (Biotic interactions hypothesis, Dobzhansky 1950; MacArthur 1972). However, given that all taxa need suitable resources and conditions to survive, species distributions must be regulated by both conditions and resources regardless of scale (Godsoe *et al.* 2015). Thus, in this tropical forest predator-prey system, biotic resources and abiotic conditions are expected to exert varying but accountable effects on harpy eagle distribution.

Here, I use a hierarchical modelling approach with four SDMs fitted as functions of abiotic conditions and food resource predictors for the harpy eagle using: **(1)** climatic and topographical predictors (Abiotic model), **(2)** solely food resource distribution predictors (Biotic model), **(3)** a combination of the two models in which food resource distributions are included, as in the Biotic model, individually (Abiotic-Biotic model), and **(4)** an Abiotic-Biotic model in which the biotic components have been reduced to a single variable reflecting prey species richness (Abiotic-SR model). Further, pair-wise niche overlaps in

geographical space were calculated and all distributions were correlated to determine commonality in distribution for all species in this predator-prey system. Lastly, using a novel analytical approach, ordination calculated in environmental space was used to determine the overall extent of niche overlap within this predator-prey system. Specifically, I sought to establish whether including food resource distributions was more important for predicting harpy eagle distribution at a continental scale than using only abiotic variables, and whether, if used in combination, biotic variables meaningfully improved climate-derived model predictions. Further, I quantified the level of niche overlap between the harpy eagle and its main prey in this lowland tropical forest predator-prey system, and predicted areas of highest environmental stability for the harpy eagle and its main food resources.

3.3 Methods

3.3.1 Occurrence data

Harpy eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, The Peregrine Fund 2018) a data information system for all raptor species. For the harpy eagle, GRIN consists of occurrence data from the Global Biodiversity Information Facility (GBIF 2019a), which are mostly eBird records (79 %, Sullivan *et al.* 2009), along with two additional occurrence datasets (Vargas González & Vargas 2011; Miranda *et al.* 2019). Food resource occurrence data were compiled from GBIF (2019b,c,d,e,f,g), following the same data cleaning method, using the five most frequent prey by genus (Miranda 2015): three and two-toed sloth (*Bradypus* & *Choloepus* spp. respectively; 53.2 %), capuchin monkey (*Cebus* & *Sapajus* spp. 8.0 %), howler monkey (*Alouatta* spp. 7.3 %), and tree porcupine (*Coendou* spp. 5.3 %). Food resources were combined into their respective genera to: (1) obtain a higher number of occurrence records for each model, and (2) as an appropriate broad scale representation of food resource distribution. Two genera were used for capuchin monkey based on a recent taxonomic assessment, with *Sapajus* (or robust capuchin) found south of the Amazon river and *Cebus* (or gracile capuchin) north of the Amazon river (Lynch Alfaro *et al.* 2011). Combined these five food resource genera comprise 73.8 % by frequency and 75.6 % of biomass, representing the majority of food resources taken by the harpy eagle across its range.

Occurrences were cleaned by removing duplicate records, and those with no geo-referenced location. Only occurrences recorded from 1960 onwards were included to temporally match the timeframe of the environmental data. For all

species occurrences, a 5 km spatial filter was applied between each occurrence point using the 'geoThin' function in the R package enmSdm (Smith 2019). Using a 5 km filter approximately matches the resolution of the environmental raster data (~4.5 km) and reduces the effect of biased sampling (Kramer-Schadt *et al.* 2013). After data cleaning, a total of 1156 geo-referenced records were compiled for the harpy eagle. Applying the 5 km spatial filter resulted in 715 harpy eagle occurrence records for use in the calibration models. Occurrence records used for the food resource species calibration models are given in Table 3.1.

Table 3.1. Number of unfiltered and filtered occurrences for food resource genera used in the food resource distribution models (GBIFb,c,d,e,f,g 2019).

Food resource genus	Primary diet type	Unfiltered	Filtered
Howler monkey *Alouatta*	Folivore/Frugivore	1841	1045
Capuchin monkey *Cebus* & *Sapajus*	Omnivore	1160	706
Three-toed sloth *Bradypus*	Folivore	547	303
Two-toed sloth *Choloepus*	Folivore	389	237
Tree porcupine *Coendou*	Folivore	269	216

3.3.2 Environmental predictors

Thirty-seven bioclimatic and topographical abiotic predictors were downloaded from the WorldClim (v1.4, Hijmans *et al.* 2005) and ENVIREM (Title & Bemmels 2018) databases at a spatial resolution of 2.5 arc-minutes (~4.5km resolution). WorldClim variables (n = 19) are generated through interpolation of average monthly weather station climate data from 1960-1990, with ENVIREM variables derived from the WorldClim bioclimatic layers. Raster layers for all species were cropped using a polygon consisting of all known range countries (including Formosa, Jujuy, Misiones and Salta provinces in northern Argentina, and

Chiapas, Oaxaca and Tabasco states in southern Mexico). This improves model predictive power by reducing the background area used for testing points used in model evaluation (Barve *et al.* 2011; Radosavljevic & Anderson 2014). Before building each model, all predictors were tested for multicollinearity underlying occurrences using Variance Inflation Factor (VIF, Hair *et al.* 2006). VIF is based on the square of multiple correlation coefficients, regressing a single predictor variable against all other predictors. A stepwise elimination of highly correlated variables was used retaining predictors with a VIF threshold of < 10 (Dormann *et al.* 2013), and Spearman's Correlation Coefficient of $r_s \leq |0.7|$ retained for consideration as predictors.

Environmental predictors for the food resource distribution models were selected based on species biology and reducing collinearity between environmental predictors underlying the occurrences of each specific food resource genus (Meineri *et al.* 2012). Using this method all five food resource models used a different set of environmental predictors (Table S3.1), resulting in low collinearity between the final food resource model raster predictors (all tests VIF = < 10; Table S3.2). Collinearity tests were calculated using the 'corSelect' function in the R package fuzzySim (Barbosa 2015, 2018) and the 'vifstep' function in the R package usdm (Naimi *et al.* 2014). For the Abiotic-Biotic SDMs, these five predictors defining modelled food resource distributions were included in the harpy eagle model calibration as raster layers as has been done in previous studies (Arajúo & Luoto 2007; Preston *et al.* 2008; Ghergel *et al.* 2018). Finally, all individual food resource models were combined into a stacked SDM (s-SDM) and the continuous suitability values summed for a continuous estimate of food resource species richness in the range 0.0 – 5.0.

For the Abiotic model (**A**) two climatic variables, Climatic Moisture Index (CMI) and minimum temperature warmest month, and one topographic variable, Terrain Roughness Index (TRI), were included as predictors. All three predictors were selected *a priori* because combined they contributed 96 % to model prediction from a previous SDM for the harpy eagle (Sutton *et al.* 2021). Food resource distributions were used in three further models, with SDMs built and fitted using the same methodology as for the Abiotic model. First, only food resource distribution predictors were used in a Biotic model (**B**). Second, modelled food resource raster predictions were included as individual biotic predictors along with the abiotic predictors in an Abiotic + Biotic model (**A+B**). Finally, the predicted prey species richness from the overlap of their predicted presence probability was used as a single biotic predictor along with the abiotic predictors in an Abiotic + (Biotic) Species Richness model (**A+SR**). Geospatial analysis was performed in R (v3.5.1; R Core Team, 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017), rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundle 2019) and sp (Bivand *et al.* 2013) packages.

3.3.3 Species Distribution Models

SDMs were fitted using penalized elastic-net logistic regression (Fithian & Hastie 2013), using a point process modelling (PPM) framework in the R package maxnet (Phillips *et al.* 2017). Elastic net logistic regression imposes a penalty (regularization) to the cloglog model shrinking the coefficients of variables that contribute the least towards zero (or exactly to zero). The complementary log-log (cloglog) transform was selected as a continuous index of environmental suitability, with 0 = low suitability and 1 = high suitability. The

maxnet package is based on the maximum entropy algorithm MAXENT (Phillips *et al.* 2017), equivalent to an inhomogeneous Poisson process (IPP; Fithian & Hastie 2013; Renner & Warton 2013; Renner *et al.* 2015). Phillips *et al.* (2017) demonstrated the cloglog transform is equivalent to an IPP and can be interpreted as a measure of relative occurrence probability proportional to a species potential abundance. Thus, the predictions here can be interpreted as estimates of relative abundance, along with estimates of distribution.

A random sample of 10,000 background points were used as pseudo-absences recommended for regression-based modelling (Barbet-Massin *et al.* 2012) and to sufficiently sample the background calibration environment (Guevara *et al.* 2018). Optimal-model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989), to determine the most parsimonious model from two key MAXENT parameters: regularization multiplier and feature classes (Warren & Seifert 2011). For all SDMs, eighteen candidate models of varying complexity were built by comparing a range of regularization multipliers from 1 to 5 in 0.5 increments, and two feature classes (Linear, Quadratic) in all possible combinations using the 'checkerboard2' method of cross-validation (*k*-folds = 5) within the ENMeval package in R (Muscarella *et al.* 2014).

Only Linear and Quadratic features were used as model terms to produce less complex and more realistic predictions (Merow *et al.* 2013; Guevara *et al.* 2018). The checkerboard cross-validation method of partitioning masks the geographical structure of the data according to latitude and longitude lines, dividing all occurrences into four spatially independent bins of equal numbers.

By masking the geographical structure of test-data the models are projected onto an evaluation region not included in the calibration process. All occurrence and background test points are assigned to their respective bins dependent on location, thus further reducing spatial auto-correlation between testing and training localities (Radosavljevic & Anderson 2014). Response curves, parameter estimates and percent contribution to model prediction were used to measure variable performance within the optimal calibration models.

3.3.4 Model evaluation

Model performance was evaluated using both threshold-independent and threshold-dependent measures (Radosavljevic & Anderson 2014). Omission rates are a threshold-dependent measure that report the proportion of training points that are outside of the model when converted into a binary prediction. Omission rates evaluate discriminatory ability and over-fitting at specified thresholds. Lower omission rates show improved discrimination between suitable and unsuitable habitats (indicating higher performance), whilst overfitted models show higher omission rates than expected by theory (Radosavljevic & Anderson 2014). A single threshold-dependent measure was calculated based on the 10% training presence omission rate (OR10) threshold. For low over-fit models the expectation for OR10 is a value close to 0.10 (Muscarella *et al.* 2014).

Continuous Boyce index (CBI, Hirzel *et al.* 2006) was used as a threshold-independent measure of how predictions differ from a random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent with a Spearman correlation (r_s) with CBI values ranging from -1 to +1, with positive values

indicating predictions consistent with observed presences, values close to zero no different than a random model, and negative values indicating areas with frequent presences having low predicted environmental suitability. CBI was calculated using five-fold cross-validation on 20 % test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019). Models were tested against random expectations using partial Receiver Operating Characteristic ratios (pROC), which estimate model performance by giving precedence to omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios range from 0 – 2 with 1 indicating a random model. Function parameters were set with a 10 % omission error rate, and 1000 bootstrap replicates on 50 % test data to determine significant ($\alpha = 0.05$) pROC values >1.0 in the R package ENMGadgets (Barve & Barve, 2013).

3.3.5 Geographical overlap and correlation

Pair-wise geographic overlaps between the harpy eagle and the five prey distributions were measured using Schoener's *D* (Schoener 1968, Warren *et al.* 2008), which ranges from 0 (no overlap) to 1 (identical overlap). To estimate the areas where all six species distributions coincide, the three harpy eagle SDM predictions that used biotic predictors (B, A+B and A+SR) were first stacked and their respective CBI scores used to calculate a weighted mean ensemble prediction. Second, the five prey distribution SDMs were also stacked into a single raster. Lastly, a measure of commonality in species distribution was then predicted by intersecting the harpy eagle ensemble prediction, with the stacked prey distribution rasters with a threshold of 0.5 using the 'stability' function in the R package sdStaf (Atauchi 2018).

3.3.6 Environmental overlap

To quantify overlap in environmental space between the harpy eagle and its five main prey species, principal component analysis (PCA) was used to directly compare species-environment relationships in environmental space (PCA-env) in contrast to geographical space using SDMs. Using the PCA-env framework of Broennimann *et al.* (2011), ordination was performed using the R package humboldt (Brown & Carnaval 2019). The same filtered occurrences were used for the harpy eagle, but all filtered prey species occurrences were combined into a single occurrence dataset. Nine predictors (eight climatic and one topographical) were used from the WorldClim and ENVIREM databases (Table S3.3). Collinearity was reduced on the entire raster area by removing non-relevant predictors and final predictor selection checked for correlations using the 'vifstep' function in the R package usdm (Naimi *et al.* 2014; VIF = < 7).

The PCA-env method was set to calibrate on a non-analogous environmental space using a minimum convex polygon around all spatially filtered occurrences on a 100 x 100 resolution grid, with a smoothed Gaussian kernel density function (bandwidth = 1). Environmental overlap was quantified on the first two principal components using Schoener's *D* statistic. Using smoothed densities allows measured overlap to be independent of grid resolution, important for unbiased estimates of niche overlap using Schoener's *D* (Broennimann *et al.* 2011). To test equivalency in shared environmental space, first a niche Equivalency Statistic was used to test for the difference ($\alpha = 0.05$) between the observed overlap scores and those under a null distribution hypothesis that the two distributions are equivalent (Warren *et al.* 2008). For the null distribution, presence points are randomly assigned to each species, and a PCA is built on

these randomized data. This is repeated a hundred times and a probability distribution is then estimated for niche overlap under the null hypothesis that both sets of species occurrences are randomly distributed in the environment. Second, to measure the power of the Equivalence Statistic to detect differences in environmental space, a Background Statistic was used to test ($\alpha = 0.05$) whether the observed occurrences of one species were more similar than expected by chance to the background occurrences of the other species (*n* = 100; Warren *et al.* 2008).

The background test corrects for the environmental heterogeneity inherent in environmental data underlying occurrence data, assuming that all species are choosing environments at random throughout their respective geographic ranges. If distributions are not equivalent, a statistically significant difference allows rejection of the null hypothesis of niche equivalency between the two distributions, regardless of the significance of the Background Statistic. A non-significant Equivalence Statistic and significant Background Statistic supports the hypothesis of equivalent shared environmental space. If both statistics are non-significant this implies niche equivalency could be the result of shared identical environmental space, with limited power for the Equivalency Statistic to detect any significant differences. Importantly, the Background Statistic assesses the power of the equivalency test by asking if two distribution models are equivalent based on the matching environments available. It does not provide any evidence that niches are not equivalent.

3.4 Results

3.4.1 Food resource distribution models

Optimal model selection ($\Delta AIC_c = 0.0$) for all prey distribution models had feature classes Linear and Quadratic as model terms and a regularization multiplier $\beta = 1$, except for two-toed sloth with $\beta = 1.5$. Discrimination ability (OR10) for all models was at, or close to expected thresholds (Table 3.2). Final best-fit models were robust to random expectations (range: pROC = 1.344-1.802) with high model calibration accuracy (range: CBI = 0.840-0.969). Capuchin monkey had the broadest distribution, followed by howler monkey and tree porcupine (Fig. 3.1). Both three-toed and two-toed sloths were largely restricted to Central America, Colombia, Amazonia and the Guiana Shield. Prey species richness was highest in Panama, north along the Caribbean coast of Central America, and south along the Pacific coast of Colombia. A broad belt of high prey species richness was predicted across northern Amazonia, east into the Guiana Shield and across the central Amazon.

Table 3.2. Evaluation metrics for prey distribution models used as biotic predictors in the harpy eagle distribution models. All models selected with $\Delta AIC_c = 0.0$. FC = feature classes: Linear (L) and Quadratic (Q), RM = regularization multiplier. OR10 = 10% training presence omission rate threshold. CBI = Continuous Boyce Index, pROC = partial Receiver Operating Characteristic ratios.

Food resource SDM	FC	RM	OR10	CBI	pROC
Capuchin monkey	LQ	1.0	0.104	0.840	1.344
Howler monkey	LQ	1.0	0.104	0.969	1.509
Three-toed sloth	LQ	1.0	0.136	0.900	1.621
Tree porcupine	LQ	1.0	0.111	0.906	1.489
Two-toed sloth	LQ	1.5	0.109	0.932	1.802

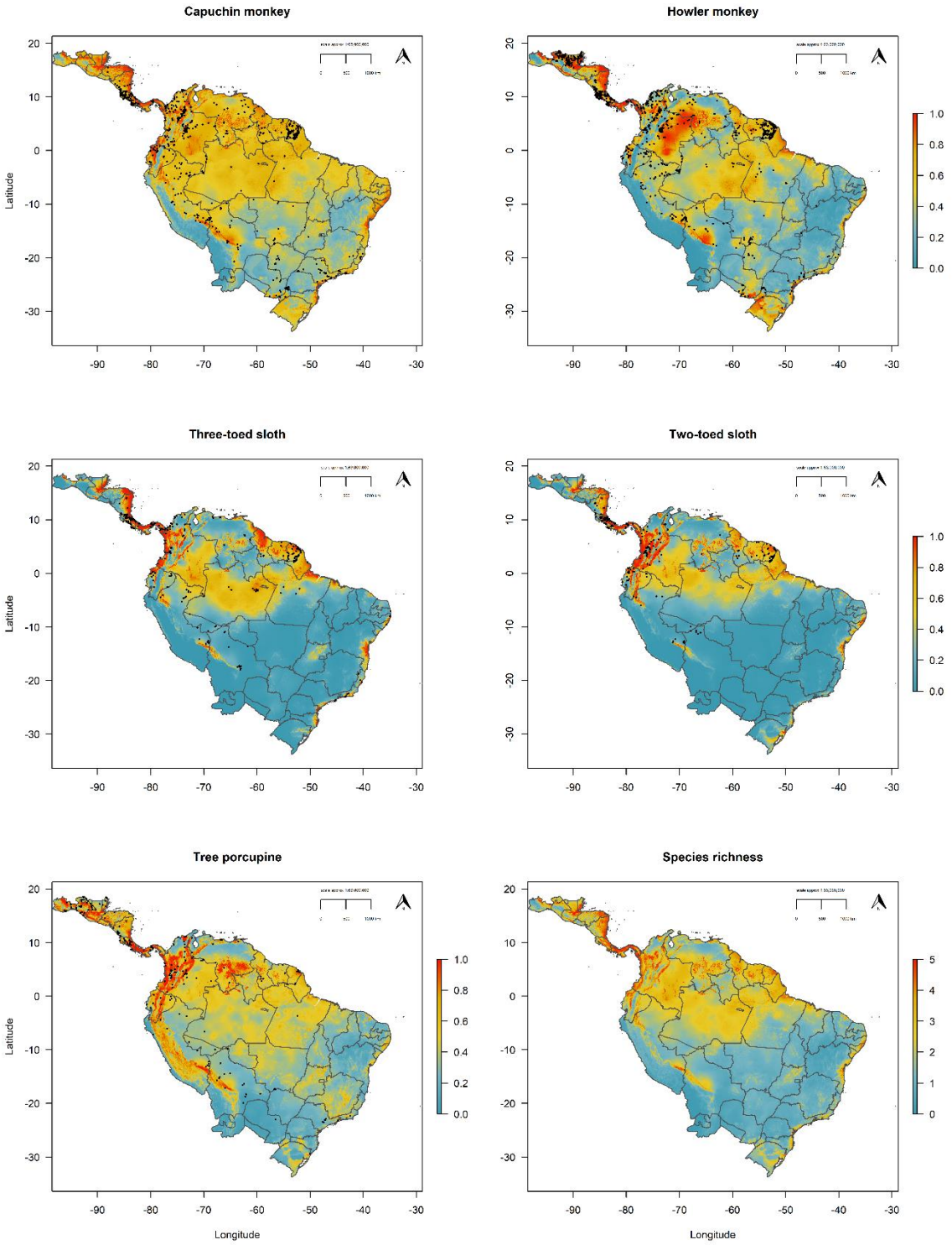


Figure 3.1. Predicted distributions for the five primary prey genera for the harpy eagle and combined into a summed prediction of prey species richness. Maps denote cloglog prediction with red areas (values closer to 1) having highest suitability. Grey borders represent national borders and state boundaries for Argentina, Brazil, and Mexico. Black points are occurrences.

3.4.2 Harpy eagle distribution models

All four best-fit harpy eagle models ($\Delta AIC_c = 0.0$) had feature classes Linear and Quadratic as model terms and a regularization multiplier $\beta = 1$. Optimal selected models had robust discrimination ability with omission rates (OR10) at expected values (Table 3.3). The A+B model had the highest model calibration performance but all models had high calibration accuracy between predicted environmental suitability and test occurrence points (range: CBI = 0.842—0.899). All models were robust against random expectations (range: pROC = 1.346-1.460). Visually, including prey distributions in both the B and A+B models constrainted harpy eagle distribution (Fig. 3.2), compared to using solely abiotic predictors. The B and A+B models captured more detail in defining areas of highest suitability and expected abundance for the harpy eagle (Fig. 3.2). This was noticeable especially across key areas of the harpy eagle range in Guyana, eastern Colombia, Panama and northern Peru and the central Amazon basin in Brazil.

Table 3.3. Model selection and evaluation metrics for all four harpy eagle SDMs ranked by lowest AIC_c. Evaluation metrics are Continuous Boyce Index (CBI) and tested against null expectations using partial Receiver Operating Characteristic ratios (pROC). OR10 = 10% training presence omission rate threshold.

SDM	AIC_c	OR10	CBI	pROC
A+B	18027.82	0.102	0.899	1.460
A+SR	18095.91	0.098	0.842	1.414
A	18119.88	0.097	0.895	1.346
B	18177.30	0.101	0.872	1.399

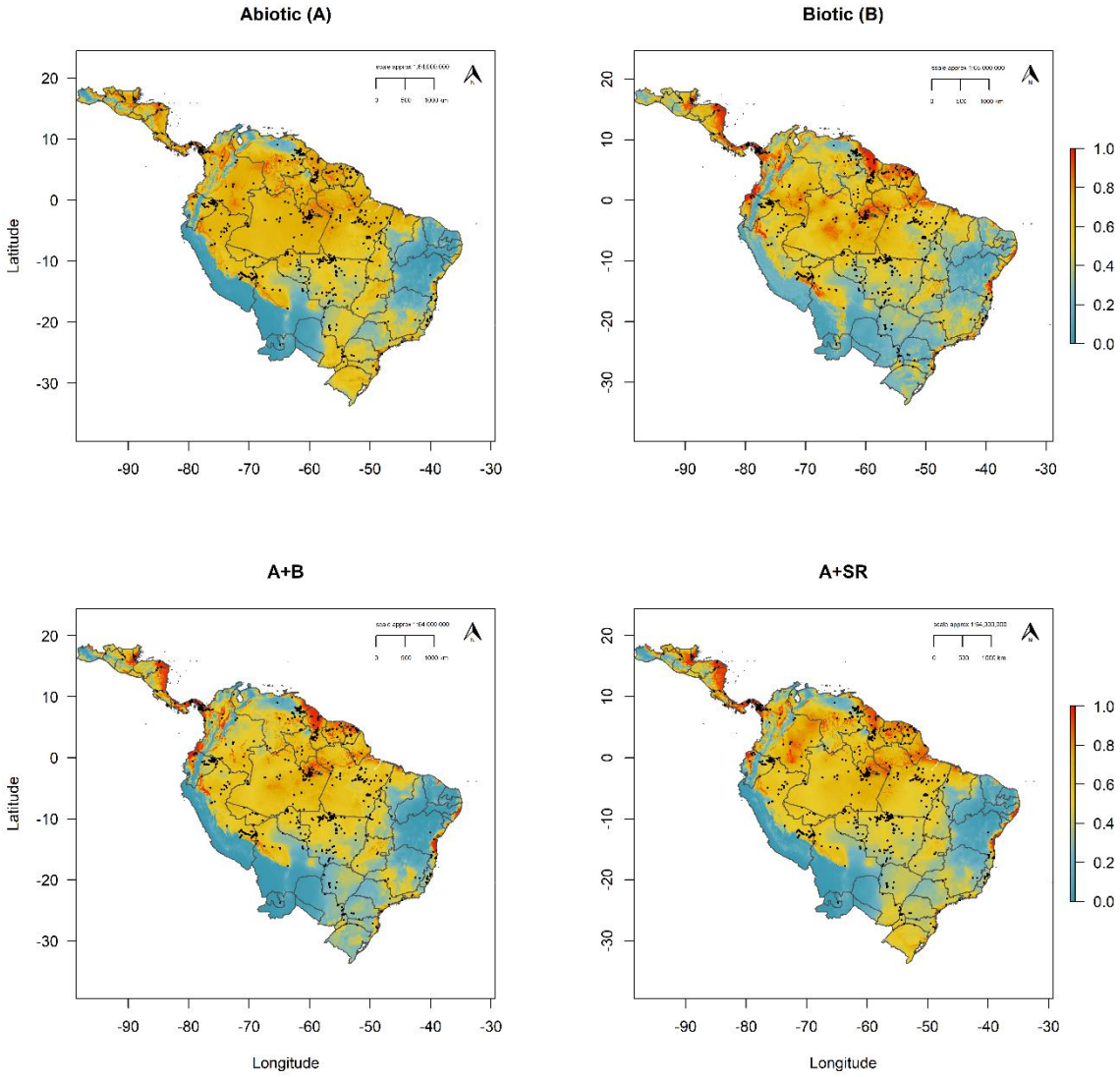


Figure 3.2. Predicted continuous distributions for the harpy eagle using abiotic and biotic predictors. Maps denote cloglog prediction with red areas (values closer to 1) having higher environmental suitability. Grey borders represent national borders and state boundaries for Argentina, Brazil, and Mexico. Black points define harpy eagle occurrences.

3.4.3 Predictor importance and responses

Climatic Moisture Index (CMI) contributed the highest percentage to the Abiotic model prediction (80.0 %), with three-toed sloth the highest contributor in both Biotic (71.3 %) and A+B (57.1 %) models. Species richness was the most important predictor (56.6 %) in the A+SR model, followed by CMI (35.2 %, Table 3.4). Model parameter estimates showed positive linear relationships with CMI in all three models using Abiotic predictors, but negative quadratic relationships (Table 3.5). Minimum temperature of the warmest month and TRI coefficients were shrunk to zero and showed no linear or quadratic relationships when biotic predictors were included. Both sloth genera had positive quadratic relationships in the Biotic model, with the relationship stronger in the A+B model, though two-toed sloth had a negative linear relationship. Tree porcupine had the strongest linear relationship in the Biotic model, followed by howler monkey, but these responses were less pronounced in the A+B model.

Table 3.4. Percent contribution to model prediction for environmental predictors used in all SDMs for the harpy eagle. Ranked by highest % contribution to the Abiotic and Biotic models.

Predictor	Abiotic	Biotic	A+B	A+SR
Climatic Moisture Index	80.0		28.6	35.2
Minimum temperature warmest month	14.7		0.1	4.3
Terrain Roughness Index	5.3		5.1	3.9
Three-toed sloth		71.3	57.1	
Tree porcupine		9.8	1.9	
Howler monkey		8.6	1.8	
Capuchin monkey		6.9	3.8	
Two-toed sloth		2.6	1.5	
Species Richness		0.8		56.6

Table 3.5. Linear and quadratic (with superscript 2) parameter estimates for each optimal model derived from penalized elastic net regression beta coefficients.

Predictor	Abiotic	Biotic	A+B	A+SR
Climatic Moisture Index	1.96		1.37	0.99
Min. temp. warmest month	0.14		0.01	0.00
Terrain Roughness Index	0.02			0.00
Climatic Moisture Index^2	-3.35		-4.70	-3.89
Min. temp. warmest month^2				0.00
Terrain Roughness Index2	0.00		0.00	0.00
Tree porcupine		6.47	1.75	
Two-toed sloth		-3.07	-2.58	
Howler monkey		2.60	0.00	
Capuchin monkey			1.71	
Tree porcupine^2		-6.90		
Howler monkey^2		-4.03	-1.38	
Capuchin monkey^2		-0.93	0.69	
Two-toed sloth^2		0.66	1.47	
Three-toed sloth^2		0.52	2.13	
Species richness^2		0.27		0.10

Response curves for predictors in the Abiotic model (Fig. 3.3) showed a unimodal response to CMI peaking at 0.4, with a positive response to minimum temperature for the warmest month peaking at suitable temperatures of 27 °C. Harpy eagle occurrence had a consistently high positive response to higher predicted values of three-toed sloth occurrence in both the Biotic and A+B models (Figs. 3.4-3.5), with positive sigmoidal responses to species richness in both the Biotic and A+SR models (Fig. 3.6). Harpy eagle occurrence responses to food resource distributions varied between models. There were positive responses to capuchin monkey occurrence in both the Biotic and A+B models, but with negative responses to two-toed sloth distribution, especially in the

Biotic model (Figs. 3.4-3.5). Howler monkey and tree porcupine had unimodal responses in the Biotic model, peaking at ~0.4 (Fig. 3.4). In the A+B model, these responses changed with a positive response to tree porcupine occurrence and a negative response to howler monkey occurrence (Fig. 3.5). The Abiotic predictor responses largely remained unchanged, when including biotic predictors, except for the sigmoidal response to terrain roughness (TRI) in both A+B models, compared to the unimodal response in the Abiotic model.

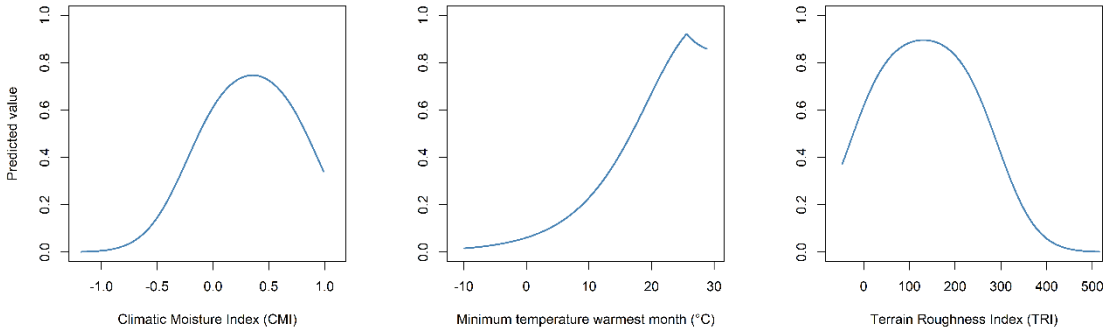


Figure 3.3. Response curves for predictors in the Abiotic distribution model for the harpy eagle.

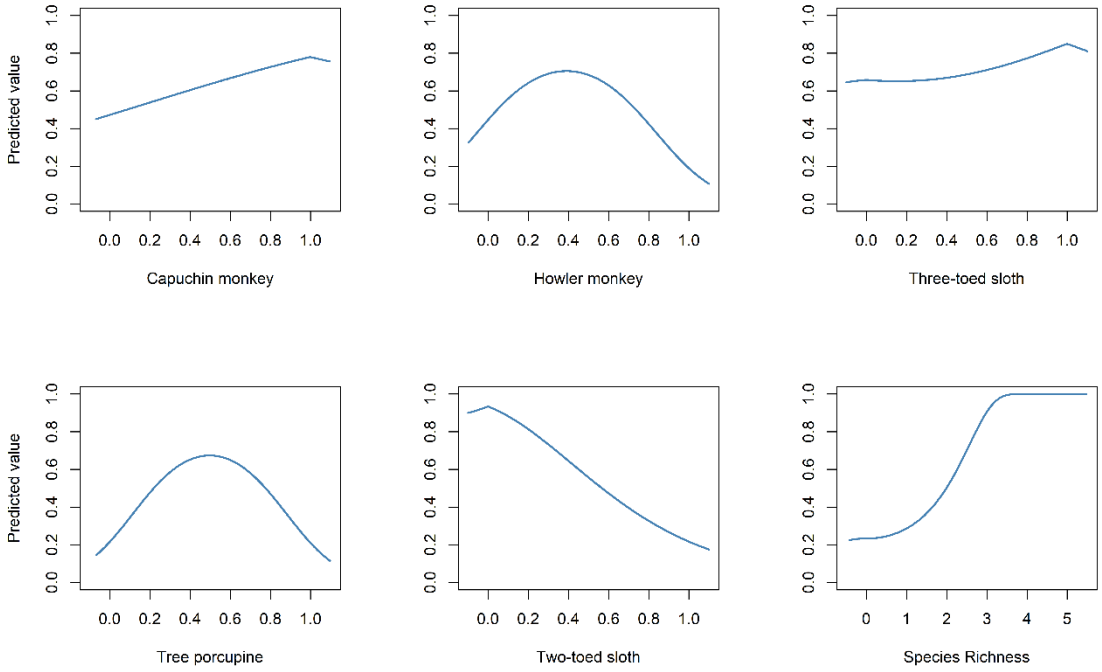


Figure 3.4. Response curves for predictors in the Biotic distribution model for the harpy eagle.

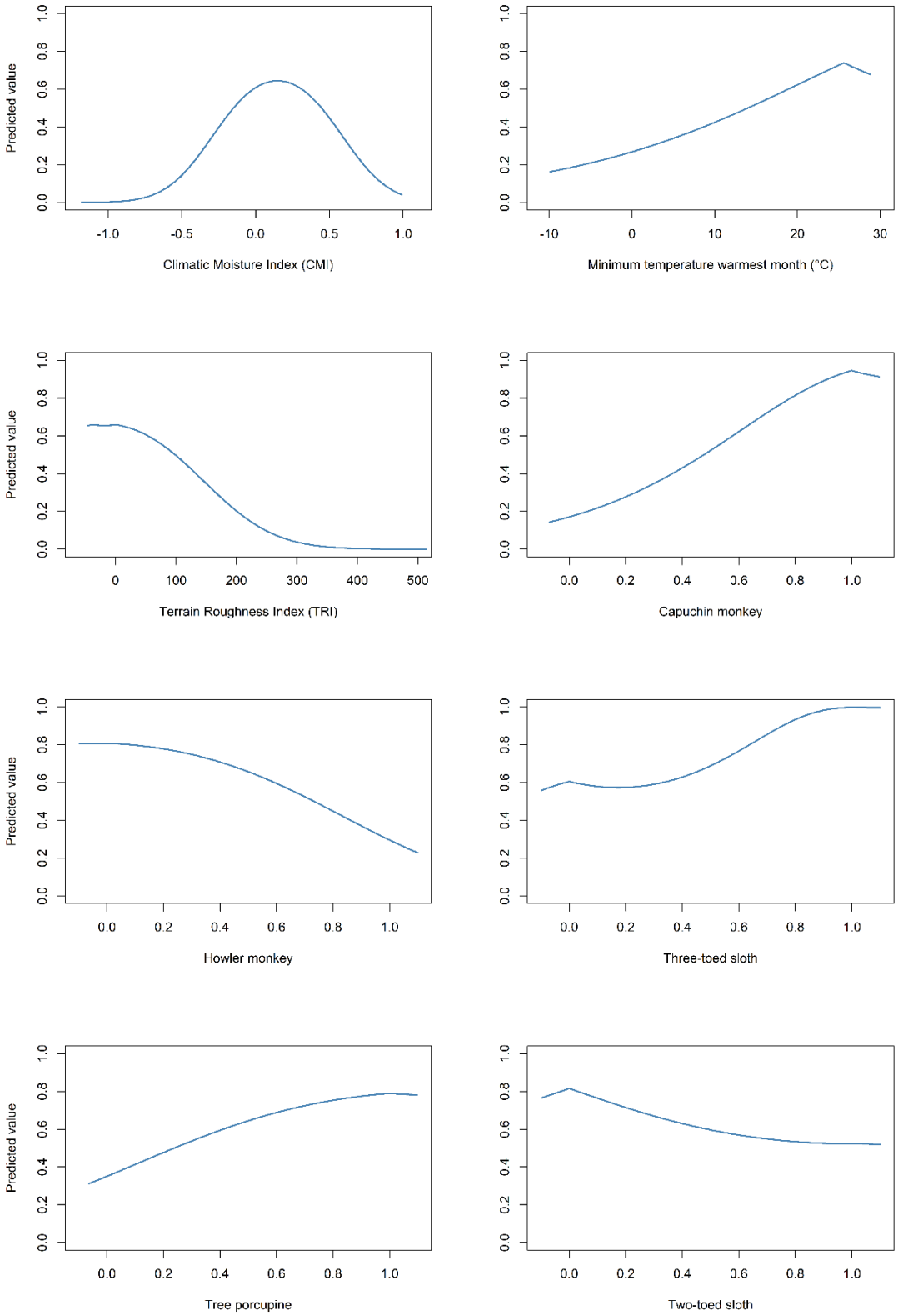


Figure 3.5. Response curves for predictors in the A+B distribution model for the harpy eagle.

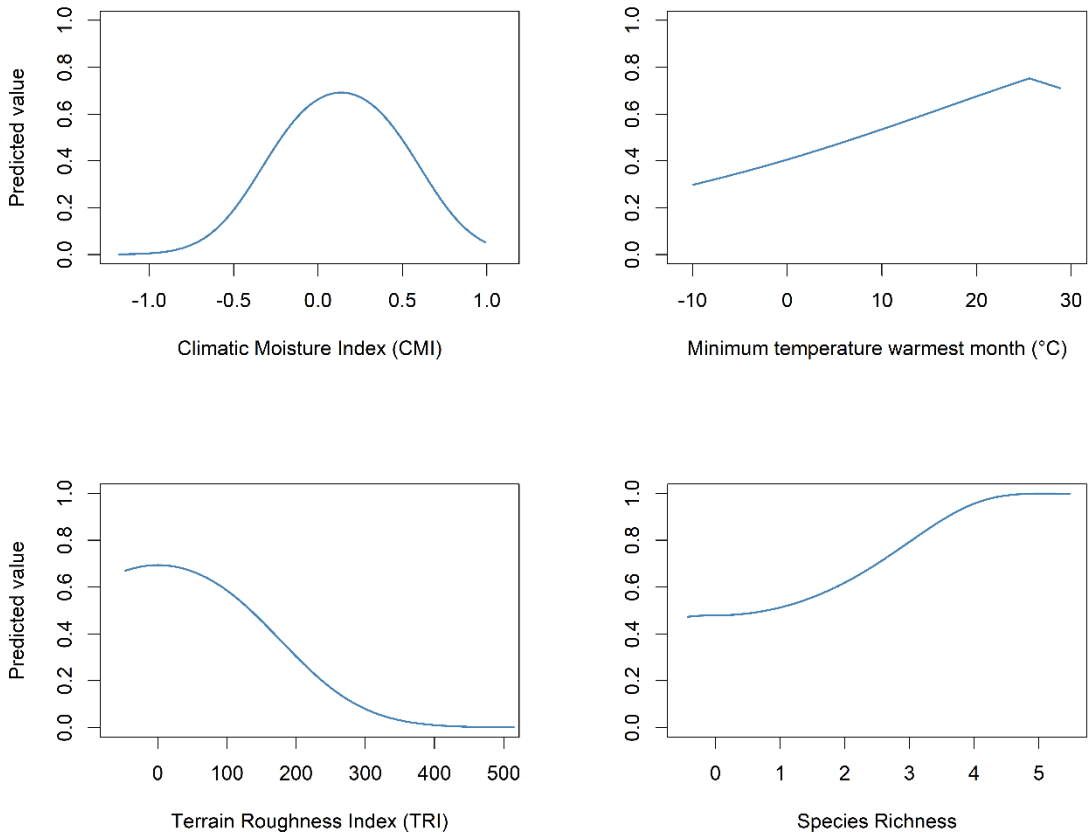


Figure 3.6. Response curves for predictors in the A+SR distribution model for the harpy eagle**.**

3.4.5 Geographic overlap and correlation

In geographic space, pair-wise overlaps between the harpy eagle and its food resource distributions were highest with capuchin (*D* = 0.867) and howler monkey (*D* = 0.858), followed by tree porcupine (*D* = 0.814). Three-toed sloth (*D* = 0.680) and two-toed sloth (*D* = 0.635) both had similar, but lower overlap scores compared to the primate and porcupine genera. The most correlated areas of distribution were first along the Caribbean coast of Central America, extending into the Chocó region along the Pacific coast of Colombia (Fig. 3.7). Second, a large but patchy area of high stability was predicted across

Amazonia, extending from eastern Colombia, across the Guiana Shield and south into the northern Amazon of Brazil.

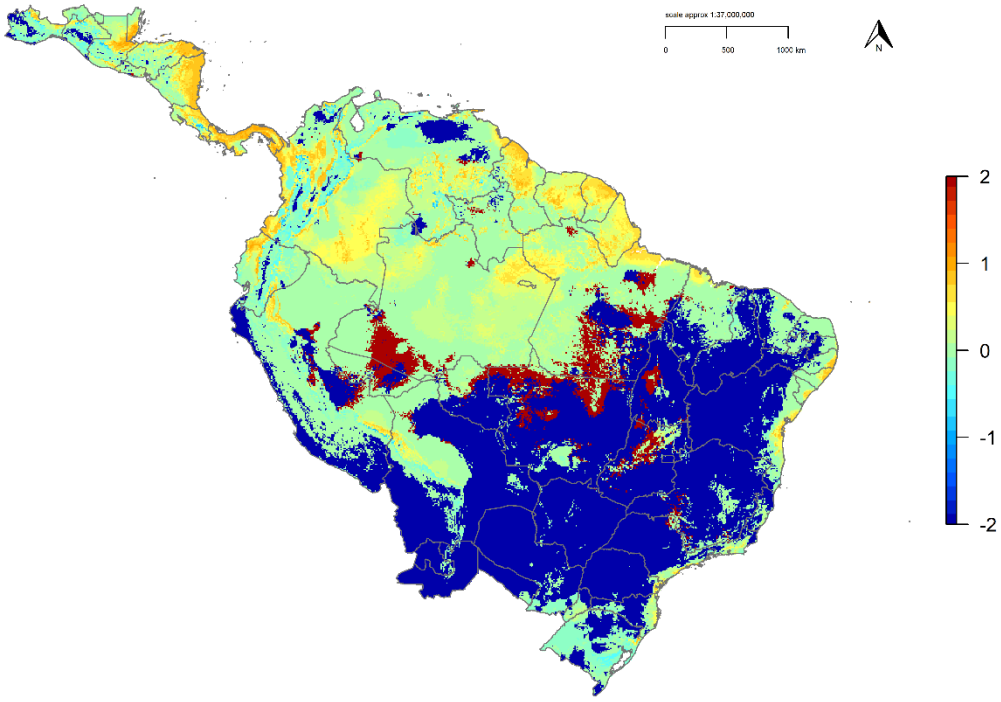


Figure 3.7. Predicted distribution correlation for the harpy eagle given the distribution of its five main prey species. Values close to -2 suggest absence, -1 to 0 can be interpreted as colonisable areas, 0 to 1 defines areas of highest suitability (prey availability) and values of 2 (dark red patches) show the most unsuitable (low prey availability) areas.

3.4.6 Environmental overlap

In environmental space the core of prey distribution overlapped with the main core area for harpy eagle distribution, but the harpy eagle also occurs outside of this core food resource range (Fig. 3.8). Measuring overlap in environmental space resulted in moderate overlap (D = 0.424), with the hypothesis of equivalence between the harpy eagle and its food resource distribution rejected from the Equivalency (p = 0.02) and Background Statistics (p = 0.267). Both the

harpy eagle and its main prey occupied more dissimilar environmental space than expected by chance, with the food resource distribution occupying a more restricted environmental space compared to the harpy eagle (Figs. S3.1-S3.2).

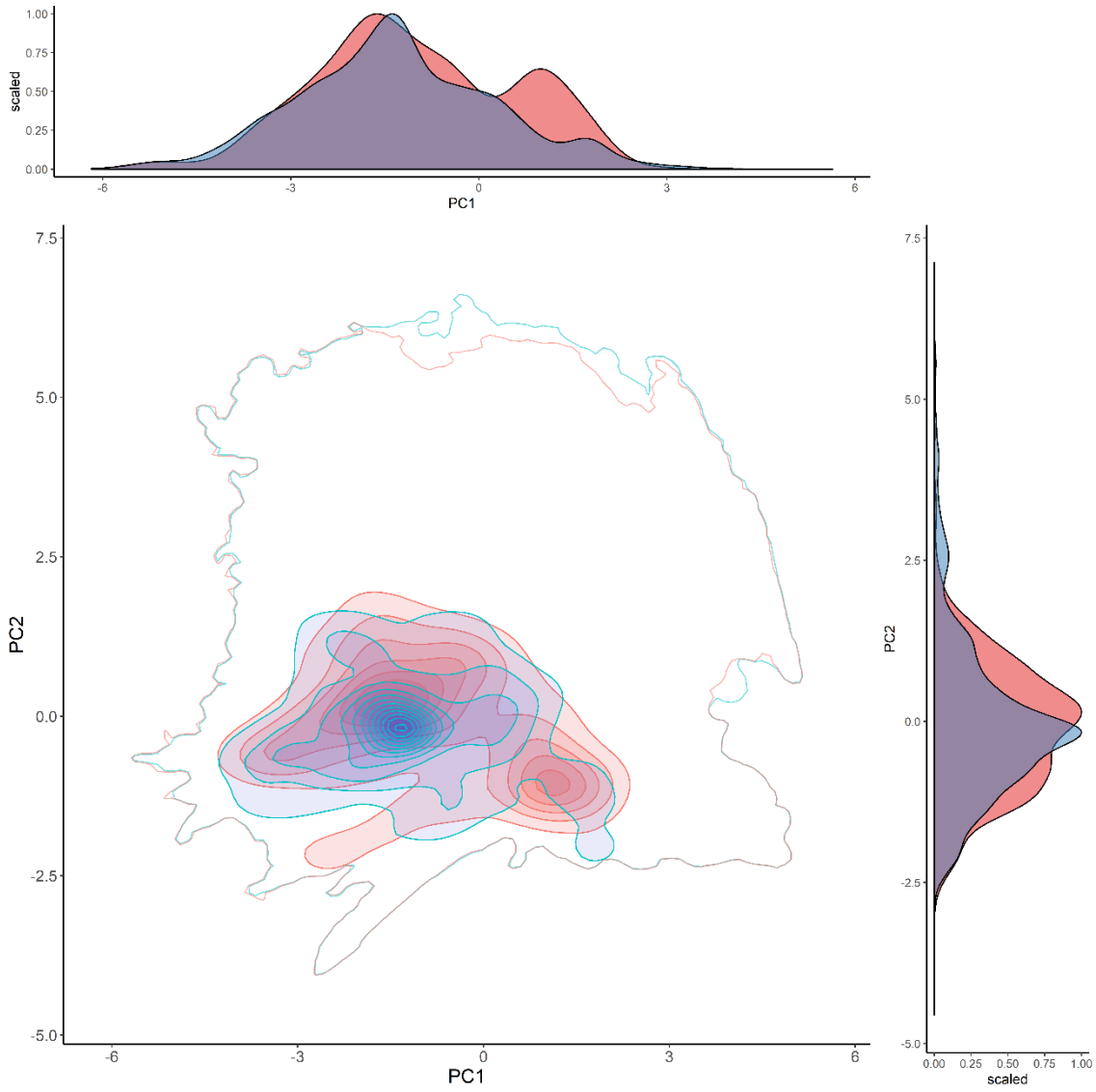


Figure 3.8. Environmental overlap (purple) for the harpy eagle (red) and its five main prey species combined (blue) across environmental space from the first two principal components.Total variance explained by the two principal components = 62.71 % (PC1 = 41.72 %, PC2 = 20.99 %). Filled isopleths are kernel densities from 1-100%. Empty kernel density isopleths represent 1% density isopleth of the environment.

3.5 Discussion

Recent theoretical and empirical work has demonstrated the importance of including resource distributions in macro-scale SDMs (Araújo & Rozenfeld 2014; Atauchi *et al.* 2018; Ghergel *et al.* 2018; Palacio & Girini 2018). The results here show that incorporating the distribution of the harpy eagle's five main prey species at a continental scale improved its distribution estimates compared to using solely abiotic predictors. This result further counters the Eltonian Noise Hypothesis (Soberón & Nakamura 2009), the assumption that biotic interactions are unimportant at broad spatial scales (Pearson & Dawson 2003). Including food resources as individual prey species distribution rasters improved the predictive performance of the Abiotic model. Moreover, using solely biotic predictors or combined as species richness still resulted in high performing models, but the combination of detailed abiotic and biotic predictors (A+B model) was best. Geographic overlap ranged from moderate to high between the harpy eagle and its main prey species. However, overlap was lower in environmental space when all main prey occurrences were combined, suggesting the harpy eagle switches to other food sources outside of core areas that enable its persistence in peripheral habitats.

The spatial pattern of species' distributions are products of physiological constraints such as climate and topography, and interactions with other co-occurring species (MacArthur 1972). It follows then that both abiotic and biotic factors combined should drive species distributions, and abiotic variables alone are unable to provide sufficient detail for distribution estimates at coarse scales (Wisz *et al.* 2013; Kass *et al.* 2019). The results here support this conclusion by improving an abiotic model prediction with the inclusion of food resource

distributions. Three-toed sloth was the most important biotic predictor in both the Biotic and A+B models (Table 3.4), consistent with sloths being the principal prey for the harpy eagle across its range (Aguiar-Silva *et al.* 2014; Miranda 2015; Miranda 2018). However, the importance of sloth distribution decreased when including abiotic factors, with CMI the second most important predictor in the A+B model. This indicates that only a reduced subset of climatic and biotic predictors are necessary to account for the major distributional constraints for the harpy eagle.

In the A+SR model, species richness was the most important predictor (56.6 %), followed by CMI (35.2 %). Combined, these two predictors accounted for nearly 92 % of model prediction, further supporting the inclusion of food resource species richness as a predictor in SDMs. Yet, when including species richness in the Biotic model its importance was low, probably due to any predictive power lost amongst the other biotic noise from the individual food resource predictors. For SDMs food resource distributions should thus be included as single predictors where predator-prey interactions are well established, and occurrence data are available. However, if occurrence data for single prey species are lacking (as is often the case), then combining all known food resource species into a single predictor is a valid method (Kass *et al.* 2019). One of the limitations of this study was only including the five main prey species when it is known that other prey species are consumed by the harpy eagle across its range (Miranda 2015). Indeed, the occurrence of suitable environmental space for the harpy eagle outside of its main food resource distributions suggests switching to other food types outside of its core range.

The results here confirm the importance of sloth distribution as one of the main drivers for harpy eagle distribution. There were high positive responses between harpy eagle distribution and three-toed sloth occurrence and both sloth genera had the highest percent contributions to the Biotic model prediction. Indeed in some parts of their range harpy eagles are sloth diet specialists (Miranda *et al.* 2020), with sloths comprising between 80-95 % of prey frequency in central and eastern Amazonia (Galetti & de Carvalho 2000; Aguiar-Silva *et al.* 2014) and north-east Ecuador (Muñiz-López 2008). However, the harpy eagle is not so specialized on a diet of sloths as to be absent from areas where sloths are not present. It seems likely that in the southern and eastern parts of the harpy eagle range primates and porcupines are the key prey species, replacing sloths as the primary food source (Miranda 2015). Thus, the models here are able to capture the spatial variation in predator-prey distribution across a continental tropical forest system by using a range of key prey genera and not relying solely on a single biotic predictor.

Using response curves to interpret model outputs is a useful though underused aspect of model evaluation in many SDMs (Guevara *et al.* 2018; Kass *et al.* 2019). Here, modelled responses for the three-toed sloth were strongly positive in both the Biotic and A+B models, peaking at 1.0 as expected (Figs. 3.4-3.5). Capuchin monkey followed similar positive responses, yet there was a negative response to two-toed sloth distribution. Given the broad distribution of the two-toed sloth closely matching that of the harpy eagle this seems counter-intuitive and it is difficult to explain this response. Both howler monkey and tree porcupine had unimodal responses in the Biotic model, peaking at 0.4. However, when all predictors were included in the A+B model, tree porcupine

showed a clear positive response. Conversely, harpy eagle distribution then showed a negative response to howler monkey distribution, opposite to the positive response in the Biotic model. This variation in model responses suggests either prey switching or highly complex interactions occurring between abiotic and biotic processes. Using methods that are capable of modelling complex species interactions (e.g. regression-based, Aragón & Sánchez-Fernández 2013; or Bayesian networks, Staniczenko *et al.* 2017) may be a way forward to tackle this problem for biotic SDMs.

3.5.2 Geographical overlap and correlation

Pair-wise geographic overlaps supported strong relationships in distribution between the harpy eagle and its main food resources. High overlaps with most of its main prey suggests harpy eagle distribution is largely dependent on where its main food resources exist. Both primate prey genera (capuchin and howler monkey) had higher overlap values than the other main prey species. This could be partly explained by both primate genera having similar broad distributions across the Neotropics to the harpy eagle, thus overlap values would be expected to be high. Conversely, overlaps for both sloth genera were lower, even though in many areas of the harpy eagle range sloths are often the primary food resource. However, both sloth genera have more restricted ranges than both the primate genera, thus overlap values would be expected to be lower. The correlation model predicted the most common areas of distribution across Amazonia, the Guiana Shield, and the Caribbean coast of Central America. Given the high reliance that harpy eagle distribution has with its main food resources, conserving tropical lowland forest habitat and prioritizing research in these regions is recommended.

3.5.3 Environmental overlap

Interestingly, when all food resources were combined in environmental space, overlap was markedly lower than any single overlap in geographical space. The harpy eagle and combined prey distributions were significantly different from each other in environmental space, suggesting that the harpy eagle is able to exist in areas outside of its main food resource distributions. Harpy eagles are known to feed on over 100 prey species and are adaptable in their food choices when required (Miranda 2015, 2018). Thus, even in areas where its main prey is not abundant, the harpy eagle is presumably still able to switch to other food types, expanding its potential distribution beyond its core range. Measuring distribution in environmental space is thus useful as a comparison to geographical space, giving a more in-depth picture across different dimensions in distribution. Complex distributional relationships between taxa can often go undetected in geographical space (Warren *et al.* 2019). Thus, comparing distributions of co-occurring taxa in environmental space provides a more comprehensive account of niche dimensions.

3.5.4 Tropical species distributions

The biotic interactions hypothesis states that species interactions are the main driver for species distribution in the relatively stable climates of the tropics (MacArthur 1972; Louthan *et al.* 2015). The results here in general support this, though abiotic processes are clearly important, with Climatic Moisture Index (CMI) still the key abiotic predictor in the A+B and A+SR models. Because CMI is closely correlated with the primary vegetation types in Neotropical forests (Beck *et al.* 2018), it seems likely that CMI is acting as a proxy for lowland

tropical forest, which by definition is the key vegetation type for all species distributions in this tropical forest system. Thus, both specific food resources and habitat type are likely the main drivers on harpy eagle distribution, which hardly seems unexpected. A useful next step would be to include direct habitat variables, competitor distributions and human impacts, along with food resources, to provide a broader perspective on the main influences determining harpy eagle distribution (Joint-SDMs, Pollock *et al.* 2014).

3.5.5 Advancing SDMs

Consistent with previous smaller scale regional studies (e.g. Hof *et al*. 2012; Aragón *et al.* 2018; Ghergel *et al.* 2018), the results here support including food resources in SDMs, suggesting that including the main food resource distributions for apex predators may be generally important at continental scales. Furthermore, these results dispute the Eltonian Noise Hypothesis, similar to conclusions from landscape to regional scale studies (Araújo *et al.* 2014; Atauchi *et al.* 2018). Taken as a whole, resource distributions accounted for most of the variation (66 % in A+B model and 57 % in A+SR model) and the more detailed model (A+B) allowed ranking of prey species importance. I contend that including resource distributions will have much practical value for advancing SDM predictions across a range of applications in space (e.g., spread of invasive species) and time (e.g., climate change range shifts). As demonstrated here, predictions were improved when applied to basic model interpolation. Not including resource distributions may result in poorer model transferability when extrapolating in space and time.

3.5.6 Conclusion

Here, I demonstrated how incorporating food resource distributions improves model predictive power and circumscribes the spatial complexity in harpy eagle distribution. Adding food resource distributions revealed the crucial role of predator-prey interactions in harpy eagle distribution. Given the wide variation in food type taken by the harpy eagle across its range (Aguiar-Silva *et al.* 2014; Miranda 2018), maintaining these prey resources should also be a priority in conservation programs for the harpy eagle. Conserving habitat for the key arboreal mammal prey populations along with one of their main predators as a complete tropical forest system seems a viable approach given the reliance on harpy eagle presence with their main food resource distributions. I encourage practitioners to incorporate known biotic interactions into SDMs, but modellers should recognise that understanding the complex interactions inherent in natural systems is a challenge (Aragón *et al* 2018). Whilst I demonstrate that using resource distributions improves model predictions at macro-scales, this needs further testing across multiple taxa and ecosystems to determine if this finding is consistent in other species.

3.6 Appendices

Appendix 1 Supplementary Tables

Table S3.1. Environmental variables used as predictors for food resource distribution models used as biotic predictors in the harpy eagle distribution models. Black points indicate which environmental variables were used in each respective species distribution model.

Predictor	Capuchin monkey	Howler monkey	Three-toed sloth	Tree porcupine	Two-toed sloth
Mean diurnal temperature range			●		●
Isothermality	●	●	●		
Mean temperature wettest quarter	●				
Precipitation wettest month				●	
Precipitation driest month	●	●			
Precipitation warmest quarter	●	●	●	●	●
Precipitation coldest quarter					
Climatic Moisture Index		●	●	●	●
Minimum temperature warmest month		●			
Maximum temperature coldest month			●		
PET driest quarter				●	●
PET seasonality					
PET warmest quarter	●	●			
PET wettest quarter	●	●	●	●	●
Topographic wetness					
Terrain Roughness Index	●	●	●	●	●

Table S3.2. Multi-collinearity test using stepwise elimination Variance Inflation Factor (VIF) for correlation between food resource distribution models used as biotic predictors.

Resource distribution model	VIF
Two-toed sloth *Choloepus*	9.260
Three-toed sloth *Bradypus*	8.732
Capuchin monkey *Cebus* & *Sapajus*	4.984
Howler monkey *Alouatta*	3.722
Tree porcupine *Coendou*	2.269

Table S3.3. Selection of variables for environmental overlap analysis using stepwise elimination Variance Inflation Factor (VIF) to reduce multi-collinearity between variables.

Environmental variable	VIF
Climatic Moisture Index	6.486
Precipitation wettest month	4.432
PET wettest quarter	3.724
PET warmest quarter	3.637
Precipitation driest month	2.933
Precipitation warmest quarter	2.684
Mean diurnal temperature range	2.037
Isothermality	1.899
Terrain Ruggedness Index	1.516

Appendix 2 Supplementary Figures

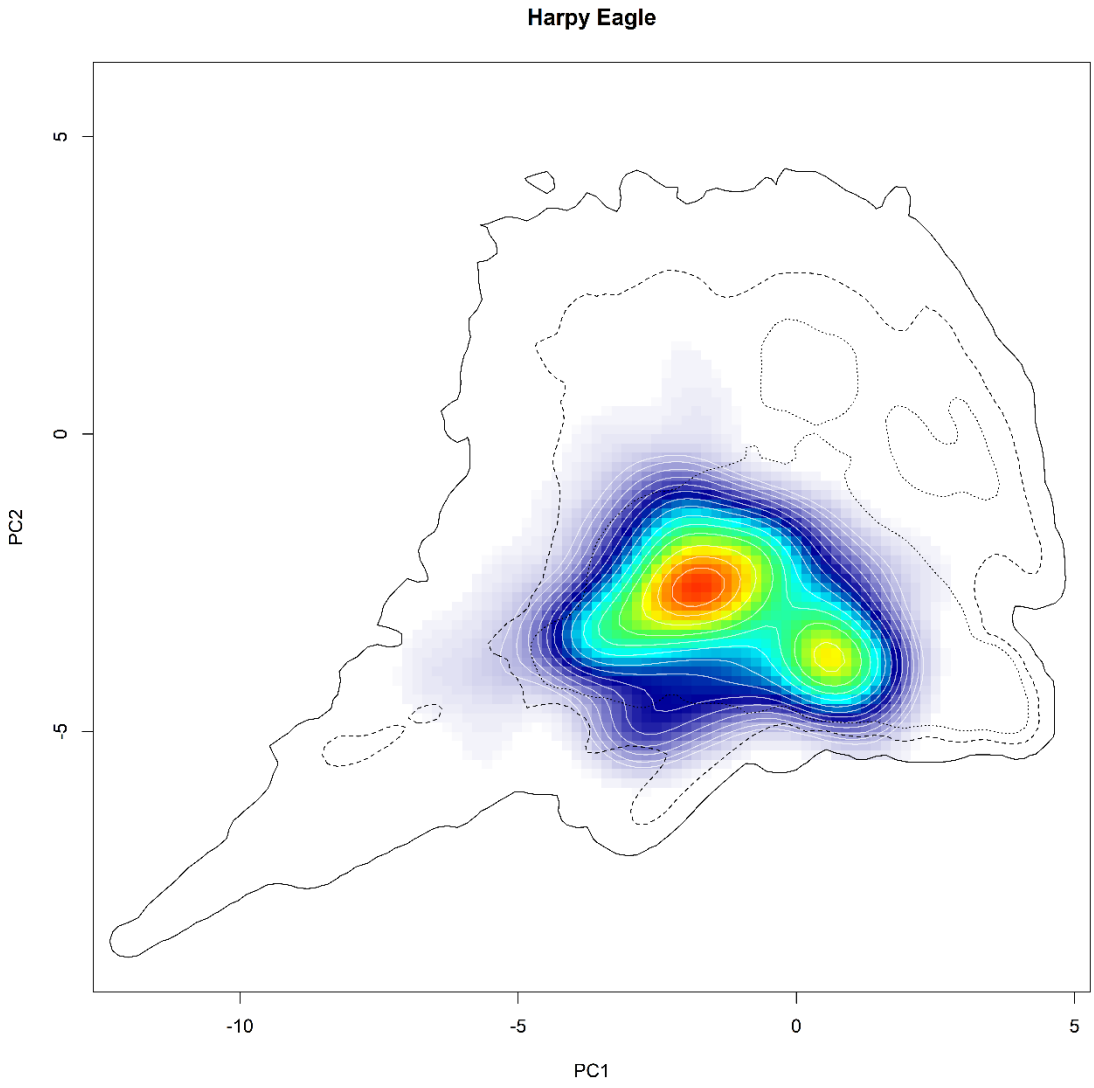


Figure S3.1. Distribution in environmental space for the harpy eagle across the first two principal components. Red areas indicate highest environmental suitability. Filled kernel density isopleths characterize kernel density values from 0.4 (blue) to 0.99 (red). Black isopleth lines define kernel density of the corresponding environment, with black solid line = 0.1, black hashed line = 0.5, black dotted line = 0.75.

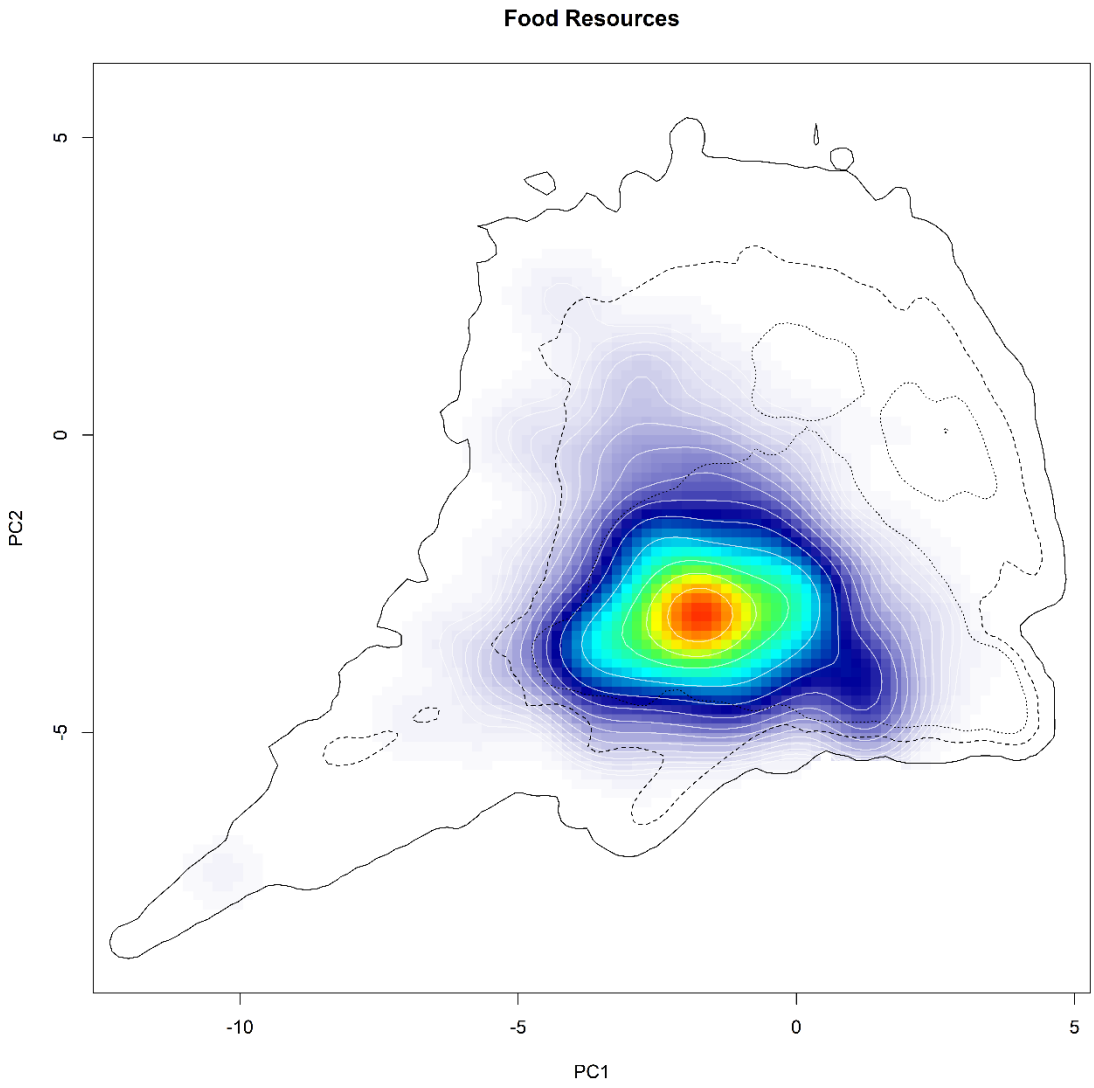


Figure S3.2. Distribution in environmental space for the food resource genera across the first two principal components. Red areas indicate highest environmental suitability. Filled kernel density isopleths characterize kernel density values from 0.4 (blue) to 0.99 (red). Black isopleth lines define kernel density of the corresponding environment, with black solid line = 0.1, black hashed line = 0.5, black dotted line = 0.75.

4. Habitat resource overlap in two sympatric Neotropical forest eagles

4.1 Abstract

Quantifying resource partitioning between pairs of co-occurring species has important ecological and evolutionary implications. Yet, few studies compare resource overlap in both geographic and environmental space. Here, I test whether the habitat requirements of two closely related Neotropical forest eagles, the crested eagle (*Morphnus guianensis*) and harpy eagle (*Harpia harpyja*), differ at multiple resolutions across their shared geographic range. Using a combination of landcover and topographic predictors, resource overlap was quantified first using generalized linear models (GLMs) at ~1 km resolution, and second using ordination at ~4.5 km resolution. The distribution of both eagles was largely explained by abundant vegetation heterogeneity and evergreen forest, but with slightly differing responses to landcover and topography. Both eagles were positively associated with evergreen forest, but with the harpy eagle more likely in areas of increased evergreen forest cover. Both eagles were negatively associated with mosaic forest cover, but this relationship was stronger for the crested eagle. Harpy eagle distribution was restricted by higher elevation and terrain ruggedness, compared to the crested eagle, whose distribution was more restricted by vegetation heterogeneity. From the GLMs, resource overlap was > 92 % in geographical space but reduced to 64 % in environmental space. From ordination, resource overlap was 76 % in environmental space, with randomization tests supporting equivalent environmental space for both eagles. These results suggest that at the biogeographical scale, the crested and harpy eagle share environmental space, but there may be subtle differences in fine-scale habitat preference.

Landcover preferences are possibly driven by diet choice which may allow co-existence and prevent direct competition. Based on these findings, I recommend environmental resource overlap is assessed in both geographical and environmental space at multiple resolutions in order to capture the inherent variability in environmental conditions available to co-occurring species.

4.2 Introduction

Climate is viewed as the major limiting factor regulating species ranges (Brown 1995), especially at broad spatial scales. However, competitive interactions and vegetation are also major drivers determining vertebrate distributions (MacArthur 1972; Cody 1974). Whilst support for climate as a key factor limiting distributions is evident (Walther *et al.* 2002; Parmesan & Yohe 2003), climatic conditions alone cannot fully explain a given species distribution (Dallas *et al.* 2017; Rich & Currie 2018), or where and how co-occurring species coexist when they have overlapping ranges (Diamond 1970; MacArthur 1972). In highly biodiverse tropical forests, closely related species may exhibit patchy, but overlapping distributions (MacArthur 1972; Robinson 1994). This may result in certain species only being able to co-exist through resource partitioning (Levins 1968; Cody 1974), where specific and subtle differences in resource and habitat requirements are met.

In Neotropical forests, raptors are amongst the least-studied bird groups due to their inherent rarity, and the difficulties of working in logistically challenging environments. Compared to temperate regions, current knowledge on the environmental drivers of distribution for many Neotropical raptors is lacking (Buechley *et al.* 2019), despite the Neotropics being a raptor diversity hotspot

(McClure *et al.* 2018). Among Neotropical forest raptors, the crested eagle (*Morphnus guianensis*) and harpy eagle (*Harpia harpyja*) have almost identical geographical ranges across Central and South America (Ferguson-Lees & Christie 2005; Gomes & Sanaiotti 2015; Miranda *et al.* 2019; Sutton *et al.* 2021). Both species are uncommon with low population densities, with the harpy eagle being on average ~1.3 times larger than the crested eagle (Ferguson-Lees & Christie 2005). Both eagles are monotypic and the only members of the subfamily Harpiinae in the Neotropics (Lerner & Mindell 2005). The Harpiinae are specialists of both primary tropical forests with a diet largely comprised of arboreal mammals and reptiles (Brown & Amadon 1968).

Generally, the crested eagle feeds on smaller prey than the harpy eagle, mainly arboreal snakes, small primates, opossums, and birds (Bierregaard 1984; Julliot 1994; Robinson 1994; Whitacre *et al.* 2012; Gomes *et al.* In press), whereas harpy eagle diet is largely comprised of large arboreal mammals, such as sloths and primates (Aguiar-Silva *et al.* 2014; Miranda 2015). Thus, crested and harpy eagles may be able to co-exist by partitioning food resources, avoiding direct competition (Sanaiotti *et al.* 2015). On a microhabitat scale, the two species may use differing forest canopy strata for breeding and hunting (Gomes *et al.* In press), with harpy eagles nesting in emergent trees (Sanaiotti *et al.* 2015) and crested eagles canopy trees (Bierregaard 1984; Whitacre *et al.* 2012). An observation of interspecific feeding of a fledged harpy eagle at its nest by a female crested eagle (Vargas González *et al.* 2006) suggests that territorial behaviour can be relaxed when both eagles exist in close proximity to each other.

Apart from localized observations reporting both Harpiinae eagles breeding within ~1-3 km of each other in similar habitats (Galetti *et al.* 1997; Muñiz-López *et al.* 2007; Sanaiotti *et al.* 2015), little is known about how these two eagles co-exist at a large biogeographical scale with highly overlapping geographic ranges. Both eagles were recorded in similar forest habitats from two landscape habitat selection studies, one in an 800-ha section of Amazonian Peru (Manu National Park; Robinson 1994), and the second along a 276 km stretch of the Xingu river in Amazonian Brazil (Sanaiotti *et al.* 2015). Harpy eagles were observed more frequently than crested eagles, suggesting the harpy eagle is the more common of the two species where both are present. From surveys along the Xingu river, Sanaiotti *et al.* concluded that territories of both eagles overlapped, but this is contrary to results from a 10,000-ha study area in French Guiana (Thiollay 1989). Here, territories of neither eagle overlapped, and Thiollay speculated that spatial segregation from its nearest competitor, the crested eagle, could explain harpy eagle rarity.

At a local level, both eagles may partition food resources and prefer different micro-habitats. However, an unanswered question is whether these patterns scale up to a broader biogeographical extent where both eagles may prefer differing habitat. Because both Harpiinae eagles co-occur within similar geographical ranges, the expectation in geographical space is for a high level of habitat resource overlap. However, given that environmental conditions are rarely equally distributed across landscapes, geographical comparisons between sister species may over-represent the overlap in environmental requirements. Therefore, when assessed in environmental space, habitat resource overlap may be lower indicating environmental niche partitioning

(Pulliam 2000; Bleyhl *et al.* 2018). Even so, given that narrow niche breadth is viewed as optimal in the relatively stable and predictable climate of the tropics (Levins 1968), both eagles are expected to have specialized environmental requirements irrespective of the level in habitat resource overlap.

Regardless of the level of individual resource overlap in environmental space, it may be more appropriate to predict distribution in geographical space at a higher phylogenetic level, combining occurrences from both Harpiinae lineages into a single dataset (Smith *et al.* 2019). Modelling at the species-level is generally the default method when using SDMs (Franklin 2009). However, this ignores evolutionary processes by following the unsupported assumption that the species is the appropriate phylogenetic level for modelling distribution (Morales-Castilla *et al.* 2017; Smith *et al.* 2019). A key issue for many spatial models is obtaining enough occurrence data from a single species to make reliable and unbiased predictions (Franklin 2009; Peterson *et al.* 2011). Combining occurrences from sister-species that have high habitat resource overlap into a single taxonomic group may result in a more useful estimate of geographical distribution by sampling over a wider environment not possible when modelling at the species-level (Morales-Castilla *et al.* 2017; Qiao *et al.* 2017).

Previous studies have reported differences in habitat use at localized scales for the crested and harpy eagle, but how environmental differences limiting distribution are perceived at broader biogeographical scales is unknown. Here, I use a multi-scale assessment across the entire environmental and geographic space available to both eagles to quantify environmental resource overlap and

preference for specific habitats. I use population-level Resource Selection Functions (RSFs) to first determine the fine-grain environmental correlates of distribution in both geographical and environmental space across the entire shared range for both eagles. Second, an environmental Principal Component Analysis (PCA-env) is used to quantify the level of coarse-grain resource overlap solely in environmental space as a comparison to using the finer-scale RSFs. Lastly, in order to determine the combined habitat range of both eagles across the widest possible sampling area, a high-resolution Habitat Suitability Model (HSM) is used to predict distribution in geographical space at the sub-family level for both Harpiinae eagles across their shared range.

4.3 Methods

4.3.1 Eagle occurrence data

Crested and harpy eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, The Peregrine Fund 2018) consisting of occurrence data from the Global Biodiversity Information Facility (GBIF 2019a,h), which are mostly eBird records (crested eagle = 75 %, harpy eagle = 79 %, Sullivan *et al.* 2009). Three additional occurrence datasets from across both the crested eagle (Gomes & Sanaiotti 2015) and harpy eagle range (Vargas González & Vargas 2011; Miranda *et al.* 2019) were also incorporated into the GRIN database. Occurrences were cleaned by removing duplicate records, and those with no geo-referenced location. Only occurrences recorded from 2000 onwards were included to temporally match the timeframe of the habitat predictors. To quantify spatial overlap in the point occurrences, a point-proximity overlap metric (*O*; Cardillo & Warren 2016) was used to test if both sets of occurrence points for each eagle species were distributed randomly and independent from each other. The point-proximity *O* metric tests for spatial overlap based on the co-aggregation in the point occurrences for each respective eagle species. The metric ranges from zero to one, with a value ~0.5 expected if the occurrence points of both species have a random and independent distribution.

Totals of 881 crested eagle records and 1065 harpy eagle records were compiled after data cleaning, with unfiltered occurrences having a moderately random distribution (*O* = 0.230, Fig. 4.1). Occurrence data for both eagle species showed similar distributions delimited in geographical space using convex hull models (Fig. S4.1). To reduce sampling bias in occurrence points for the RSFs and the HSM a 1 km spatial filter was applied between each

occurrence point using the ‘geoThin’ function in the R package enmSdm (Smith 2019). Using a 1 km filter approximately matches the resolution of the raster data (~1 km) and reduces the effect of biased sampling (Kramer-Schadt *et al.* 2013). Applying the 1 km spatial filter resulted in 439 occurrences for the crested eagle and 801 occurrences for the harpy eagle. Spatially filtered occurrences for both eagle species were distributed randomly and independent from each other (O = 0.448) compared to the unfiltered occurrences.

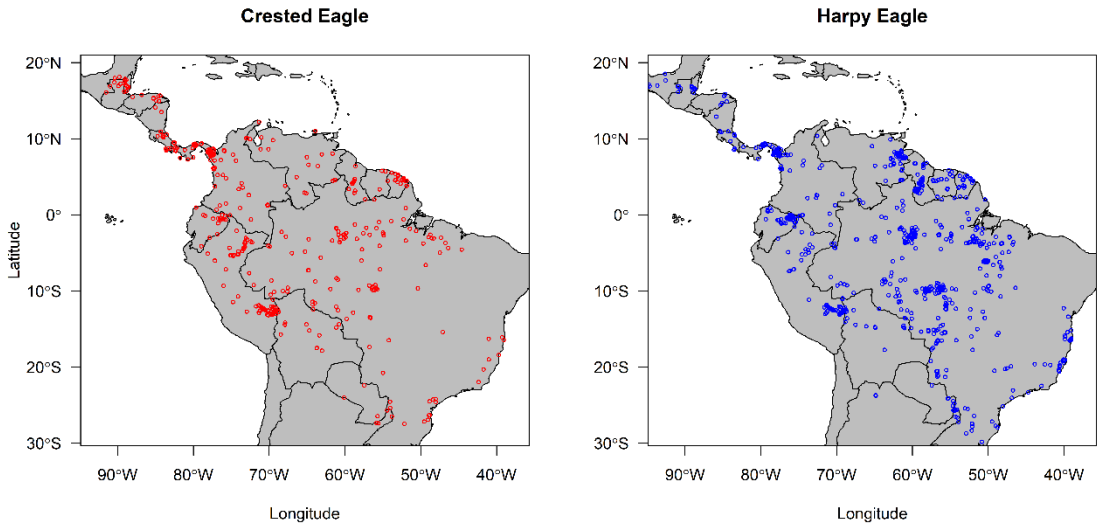


Figure 4.1. Distribution of crested eagle and harpy eagle unfiltered occurrences across Central and South America.

4.3.2 Environmental predictors

Current distribution maps show both crested and harpy eagles exist in similar geographical space (Fig. 4.1, Ferguson-Less & Christie 2005), thus the expectation is for their respective distributions to be limited by the same environmental factors. Potential predictors representing topography, vegetation heterogeneity, and landcover were downloaded from the ENVIREM (Title & Bemmels 2018) and EarthEnv (www.earthenv.org) databases. Biologically

relevant predictors were selected *a prioiri* based on the key limiting environmental factors related theoretically and empirically to each species distribution in lowland tropical forests (Vargas González *et al.* 2006; Whitacre *et al.* 2012; Sanaiotti *et al.* 2015; Miranda *et al.* 2019). A total of six continuous predictors (Table 4.1) were included in the RSF and HSM analyses at a spatial resolution of 30 arc-sec (~1km resolution). Raster layers were cropped using a delimited polygon consisting of all known range countries (including the states of Formosa, Jujuy, Misiones and Salta in northern Argentina, and the states of Chiapas, Oaxaca and Tabasco in southern Mexico), further improving model predictive power by reducing the background area used for testing points used in model evaluation (Radosavljevic & Anderson 2014).

Table 4.1. Habitat predictors used in all spatial and modelling analyses for the crested and harpy eagle.

Predictor	Source	Citation
Cultivated (%)	EarthEnv	Tuanmu & Jetz 2014
Elevation (m)	EarthEnv	Amatulli *et al.* 2018
Evergreen forest (%)	EarthEnv	Tuanmu & Jetz 2014
Homogeneity (0.0-1.0)	EarthEnv	Tuanmu & Jetz 2015
Mixed trees (%)	EarthEnv	Tuanmu & Jetz 2014
Terrain Ruggedness Index (TRI)	ENVIREM	Title & Bemmels 2018

The EarthEnv database is a repository for global environmental data derived from satellite remote sensing, including vegetation heterogeneity and landcover layers. The ENVIREM dataset includes two further topographic predictors as an addition to EarthEnv. Homogeneity is a vegetation heterogeneity texture measure indicating spatial heterogeneity of vegetation on a scale of 0.0 to 1.0 derived from the Enhanced Vegetation Index (EVI), sourced from the Moderate

Resolution Imaging Spectroradiometer (MODIS; https://modis.gsfc.nasa.gov/). Homogeneity values of zero indicate areas of lowest vegetation homogeneity, with values of one indicating areas of highest vegetation homogeneity. The three measures of percentage landcover (Evergreen Forest, Mixed Trees, Cultivated) are consensus products integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) at 30 arc-sec (~1km) spatial resolution. Mixed trees represents a mosaic of forest, shrubland and grassland. Full details on methodology and image processing can be found in Tuanmu & Jetz (2014) for the landcover layers, and Tuanmu & Jetz (2015) for the habitat heterogeneity texture measures.

After selecting biologically relevant predictors, all six candidate variables were tested for multicollinearity using Variance Inflation Factor (VIF) analysis in the R package usdm (Naimi *et al.* 2014). VIF is based on the square of multiple correlation coefficients, regressing a single predictor variable against all other predictors. A stepwise elimination of highly correlated variables was used retaining predictors with a VIF threshold of < 5, considered as suitable for multi-variable correlation (Dormann *et al.* 2013). The remaining variables were then checked for collinearity using Spearman's Correlation Coefficient with a threshold of r_s = |0.7|. All the selected variables showed low collinearity and thus all were included as predictors in model calibration (Table S4.1).

4.3.4 Resource Selection Functions

RSFs were calibrated for each species using logistic regression fitted with generalised linear models (GLMs) with a binomial logit link function in the ENMTools (Warren *et al.* 2019b) and stats R packages (R Core Team, 2018).

The RSFs followed geographical range first-order selection (Johnson 1980) using design I in a use-availability sampling protocol (Manly *et al.* 2002; Johnson *et al.* 2006; Thomas & Taylor 2006). GLMs were fitted with iteratively reweighted least squares to derive maximum likelihood estimates on model parameters, with no interaction terms. Linear and quadratic polynomial terms were fitted dependent on the scaled responses from fitting both terms on an initial model. Only linear terms were used when the quadratic term resulted in biologically unrealistic U-shaped curves, or when a linear term was sufficient to explain the scaled response. All predictors were standardized with a mean of zero and standard deviation of one. Background-absence points were randomly sampled using 10,000 points suitable for regression-based modelling (Barbet-Massin *et al.* 2012) and weights assigned equally to both presence and background points. To test calibration accuracy the explained variance from each logistic model was measured using McFadden's adjusted R^2 (R^2_{adj}, McFadden 1974).

To test discrimination ability in environmental space, a new implementation of the AUC (Area Under the Curve) statistic was calculated (referred to here as AUC_{env}) using the 'env.evaluate' function in the R package ENMTools (Warren *et al.* 2019b). AUC_{env} uses Latin hypercube sampling to estimate model fit in environmental space using all possible environmental combinations, evaluating model performance between presence and background-absence points within the minima and maxima of the environmental predictors. An $AUC_{env} = 1.0$ indicates maximum predictive model performance, with an $AUC_{env} = 0.5$ being no better than a random prediction. Given the inherent spatial autocorrelation and environmental heterogeneity present in biodiversity inventory data, a

Monte-Carlo randomization test was used to test for significance in the AUC evaluation metrics against null random expectations (Raes & ter Steege 2007). Random null models were set to calculate 95 % AUC Confidence Intervals (CI) on a frequency histogram, randomly drawing points without replacement on 100 replicates using 20 % test data under the same environmental parameters used in the best-fit models. With fitted 95 % CI AUC values, model accuracy was assessed on being significantly higher than expected by chance ($\alpha = 0.05$). Marginal response plots were used to assess environmental differences between both eagle species and biological realism of the fitted models (Guevara *et al.* 2017). Marginal responses show the response of an RSF to the environmental predictor with all other predictors held at their mean in the available environment.

4.3.5 Resource overlap

RSFs

First, to quantify the level of resource specialization for both eagles, niche breadth was measured using Levins (1968) standardized *B*2 statistic for each GLM in geographic (*gB2*) and environmental (*eB2*) space given a vector of habitat suitability scores. Niche breadth was measured on a scale from 0 to 1, with zero indicating low niche breadth (habitat specialist) and 1 high niche breadth (habitat generalist) (Krebs 1999). Second, pair-wise niche overlap metrics were calculated on each respective GLM in both geographic and environmental space to quantify similarity between models using Schoener's *D* (Schoener 1968, Warren *et al.* 2008). Schoener's *D* measures niche similarity between environmental conditions ranging from 0 (no overlap) to 1 (identical predictions). Niche breadth and overlap measures were calculated based on

Monte Carlo integration using continuous predictions in the R package ENMTools (Warren *et al.* 2019a,b).

PCA-env ordination

For the PCA-env, the same six predictors (Table 4.1) were included at a spatial resolution of 2.5 arc-minutes (~4.5km resolution). All 30 arc-sec (~1 km resolution) landcover layers were thus resampled to a spatial resolution of 2.5 arc-minutes using bilinear interpolation. Occurrences were thinned using a 5 km spatial filter to approximately match the resolution of the raster data (~4.5 km). Applying the 5 km spatial filter resulted in 353 occurrences for the crested eagle and 606 occurrences for the harpy eagle. The 5 km filtered occurrences for both eagle species had a random and independent distribution (O = 0.525) compared to the unfiltered occurrences.

Ordination techniques such as principal component analysis (PCA) use direct comparisons of species-environment relationships in environmental space in contrast to predictive resource overlap analysis using RSFs. Using the PCA-env framework of Broennimann *et al.* (2011), ordination was calculated using the R package humboldt (Brown & Carnaval 2019). The PCA-env method was set to calibrate on a non-analogous environmental space using a minimum convex polygon around all spatially filtered occurrences on a 100 x 100 resolution grid, with a smoothed Gaussian kernel density function (bandwidth = 1) to account for spatial auto-correlation. Niche overlap was quantified on the first two principal components using Schoener's D statistic. Using smoothed densities allows measured overlap to be independent of grid resolution, important for

unbiased estimates of niche overlap using Schoener's *D* (Broennimann *et al.* 2011).

To test equivalency in shared environmental space, first a niche Equivalency Statistic was used to test for the difference ($\alpha = 0.05$) between the observed overlap scores and those under a null distribution hypothesis that the two distributions are equivalent (Warren *et al.* 2008). For the null distribution, presence points are randomly assigned to each species, and a PCA is built on these randomized data. This is repeated a hundred times and a probability distribution is then estimated for niche overlap under the null hypothesis that both sets of species occurrences are randomly distributed in the environment. Second, to measure the ability of the Equivalence Statistic to detect differences in environmental space, a Background Statistic was used to test for the difference ($\alpha = 0.05$) if the observed occurrences of one species are more similar than expected by chance to the background occurrences of the other species (*n* = 100; Warren *et al.* 2008).

The background test corrects for the environmental heterogeneity inherent in environmental data underlying occurrence data, assuming that all species are choosing environments at random throughout their respective geographic ranges. If distributions are not equivalent, a statistically significant difference allows rejection of the null hypothesis of niche equivalency between the two distributions, regardless of the significance of the Background Statistic. A non-significant Equivalence Statistic and significant Background Statistic supports the hypothesis of equivalent shared environmental space. If both statistics are non-significant this implies niche equivalency could be the result of shared

identical environmental space, with limited power for the Equivalency Statistic to detect any significant differences. Importantly, the Background Statistic assesses the power of the equivalency test by asking if two distribution models are equivalent based on the matching environments available. It does not provide any evidence that niches are not equivalent.

4.3.6 Habitat Suitability Model

For the high-resolution (~1 km) Harpiinae HSM, unfiltered occurrences for both eagles were combined into a single dataset (*n* = 1,946), with a reduced subset of 1147 occurrences used in model calibration after applying a 1 km spatial filter (see section 4.3.1). The HSM was fitted using logistic regression with a logit link function using a binomial error term as a generalised additive model (GAM) in the R package mgcv (Wood 2011, 2017). GAMs are a semi-parametric extension of a GLM able to fit flexible responses to non-linear data, and thus well-suited to complex species-environment relationships (Suárez-Seoane *et al.* 2002; Granadeiro *et al.* 2004; Leathwick *et al.* 2006). The GAM included cubic regression spline smoothers on all predictors via restricted maximum likelihood to control complexity of the smoother terms (Saeedi *et al.* 2019). Maximum number of degrees of freedom for each smoother term were set at 6 and gamma = 1.4 to avoid over-fitting the data whilst still allowing some complexity in the functions (Pearce & Ferrier 2000; Granadeiro *et al.* 2004; Kim & Gu 2004). Interaction terms were not included as they often reveal complex terms in GAMs, ecologically difficult to interpret (Suárez-Seoane *et al.* 2002; Granadeiro *et al.* 2004). Due to cubic regression splines directly interpreting model parameters, no re-scaling of predictors was performed (Lancaster & Šalkauskas 1986).

Background-absence data were randomly sampled using 10,000 points suitable for regression-based modelling (Barbet-Massin *et al.* 2012), to avoid under-sampling in a restricted extent and over-sampling over too broad an area (VanDerWal *et al.* 2009) and weights assigned equally to both presence and background points. The GAM was evaluated using Continuous Boyce index (CBI, Hirzel *et al.* 2006), as a measure of how predictions differ from a random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent with a Spearman correlation (r_S) with CBI values ranging from -1 to +1, with positive values indicating predictions consistent with observed presences, values close to zero no different than a random model, and negative values indicating areas with frequent presences having low predicted environmental suitability. CBI was calculated using five-fold cross-validation on 20% test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019).

The continuous GAM prediction was reclassified to a discrete threshold prediction using low, medium and high quantile classes representing habitat suitability for both Harpiinae eagles. Lastly, class-level landscape metrics were calculated on the discrete quantile classes to estimate total and core area of habitat in the R package SDMTools (VanDerWal *et al.* 2014), based on the FRAGSTATS program (McGarigal *et al.* 2002). Core areas were defined as those cells with edges wholly within each habitat class, with cells containing at least one adjacent edge to another class cell considered as edge habitat. General model development and geospatial analysis were performed in R (v3.5.1; R Core Team, 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017),

rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundle 2019) and sp (Bivand *et al.* 2013) packages.

4.4 Results

4.4.1 Resource Selection Functions

Both GLMs had high discrimination ability (crested eagle: AUC_{env} = 0.992, harpy eagle = AUC_{env} = 0.992), with randomization tests robust against null expectations ($p < 0.03$; Fig. S4.2). Both species were limited by similar environmental factors, though the likelihood and strength of each predictor varied between the two species. Both were negatively associated with homogeneous vegetation, indicating preference for areas of high heterogenous vegetation. Both eagles were more likely to be positively associated with evergreen forest, though its importance was lower for the crested eagle. Both eagles had negative responses to cultivated areas, with a stronger negative association for the harpy eagle. The harpy eagle was more negatively associated with higher elevation compared to the crested eagle.

For the crested eagle, five predictors had significant terms (Table 4.2), with the full model able to explain 88 % of the variability in environmental space (R^2_{adj} = 0.88). Crested eagles were more likely to be negatively associated with homogeneous vegetation, mixed tree cover, elevation, and cultivated areas, but positively associated with evergreen forest. For the harpy eagle, seven predictors had significant terms (Table 4.2), with the full model able to best explain 86 % of the variability in environmental space (R^2_{adj} = 0.86). Harpy eagles were more likely to be positively associated with evergreen forest, and negatively associated with elevation, with responses to both these predictors stronger compared to the crested eagle. The harpy eagle had similar negative associations with homogeneous vegetation and mixed tree cover, as the crested eagle.

Table 4.2. GLM terms derived from maximum likelihood estimates obtained from each respective species model. Predictors ranked by the value of regression coefficient estimates. Superscript 2 indicates quadratic model terms.

Crested eagle

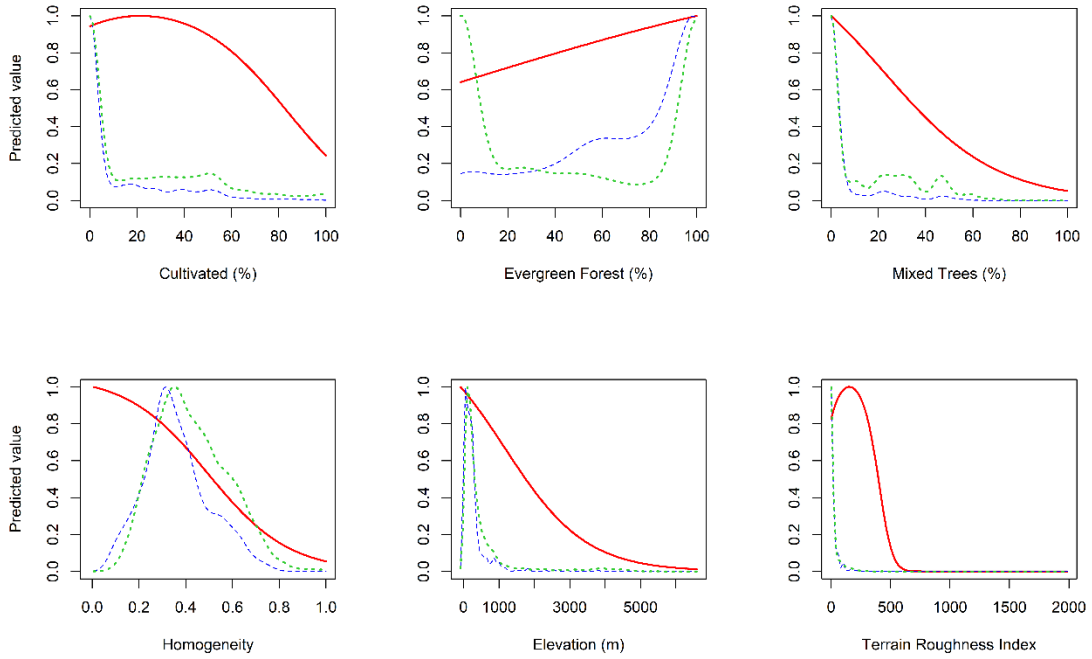
Predictor	Estimate	SE	*z*	*p*
Intercept	-0.78	0.12	-6.41	<0.001
Homogeneity	-87.37	11.21	-7.79	<0.001
Elevation	-81.01	25.21	-3.21	0.001
Mixed Trees	-73.64	17.51	-4.21	<0.001
Evergreen Forest	63.93	21.73	2.94	0.001
Terrain Roughness Index^2	-30.25	35.93	-0.84	0.400
Cultivated^2	-29.58	12.89	-2.29	0.021
Cultivated	-22.79	16.78	-1.36	0.174
Terrain Roughness Index	9.18	19.02	0.48	0.629

Harpy eagle

Predictor	Estimate	SE	z	*p*
Intercept	-0.97	0.11	-8.72	<0.001
Elevation	-157.46	27.98	-5.63	<0.001
Evergreen Forest	81.12	17.68	4.59	<0.001
Homogeneity	-73.97	8.48	-8.72	<0.001
Mixed Trees	-44.15	13.77	-3.21	0.001
Cultivated	-41.92	15.32	-2.74	0.006
Cultivated^2	-36.56	12.55	-2.91	0.004
Terrain Roughness Index^2	-33.19	14.48	-2.29	0.021
Terrain Roughness Index	23.97	0.11	1.61	0.107

Overall, responses in distribution to habitat were consistent for both the crested and harpy eagle, with similar responses to vegetation heterogeneity and topography and restricted tolerances for higher terrain roughness (Fig. 4.2). Both eagles were negatively associated with areas of high vegetation homogeneity, indicating similar preference for more heterogeneous vegetation. Responses to the three landcover predictors, however, differ subtly. Both eagles had high peak suitability of 100 % evergreen forest cover, but the response was flatter for the crested eagle compared to the harpy eagle. For mixed tree cover, the crested eagle showed a steeper negative response to higher percent cover, compared to the weaker negative response from the harpy eagle. For cultivated areas, both eagles had fairly broad tolerances but with highest suitability in areas with ~20 % cultivation cover.

Crested eagle



Harpy eagle

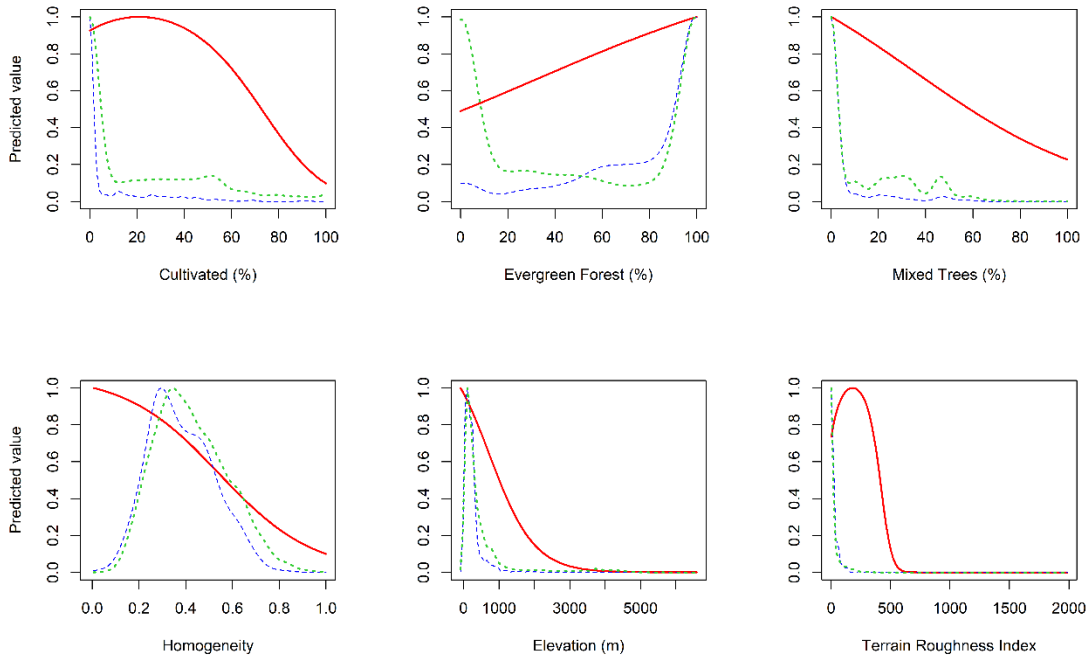


Figure 4.2. Marginal responses for each respective species model from all continuous GLM predictors. Red lines indicate environmental suitability, blue dashed line presence locations and green dotted line background locations.

4.4.4 Environmental overlap

From the GLMs both eagles had similar niche breadth across geographical space, with crested eagle niche breadth marginally higher (*gB*2 = 0.692), than the harpy eagle (*gB*2 = 0.662). In environmental space, niche breadth was markedly reduced for both the crested eagle (*eB*2 = 0.034) and harpy eagle (*eB*2 = 0.018). Resource overlap across geographical space from the GLMs was high (*D* = 0.925), but moderate across environmental space (*D* = 0.639). Measuring overlap in environmental space using the coarser-grain PCA-env resulted in moderate overlap (*D* = 0.762, Fig. 4.3), with both eagles sharing equivalent environmental space supported from the combination of a non-significant Equivalency Statistic (*p* = 0.79) and significant Background Statistics (*p* = 0.01, see section 4.3.5). Both eagles occupied more similar environmental space than expected by chance, with the harpy eagle occupying a slightly more restricted environmental space compared to the crested eagle (Fig. 4.4).

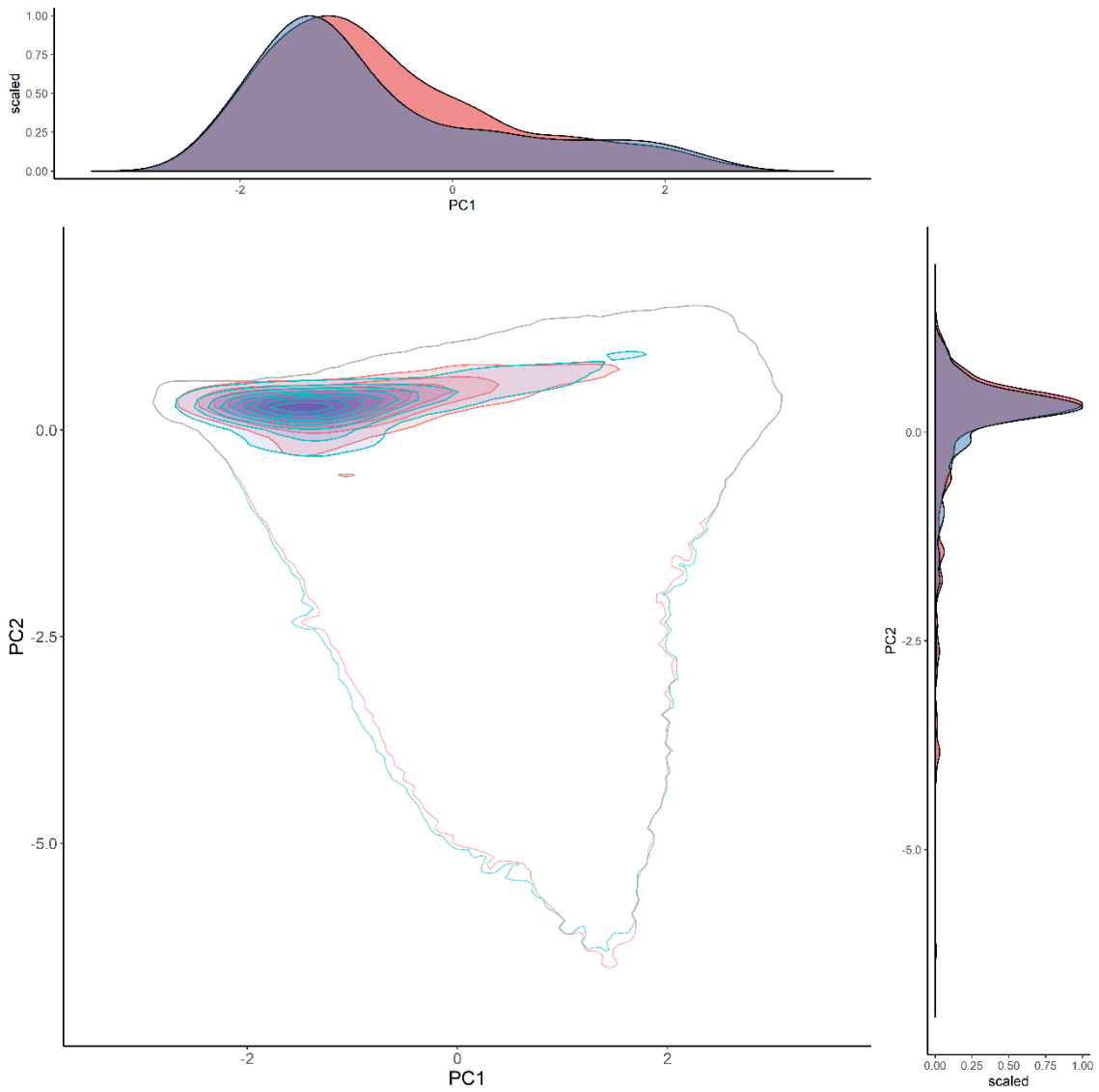


Figure 4.3. Environmental overlap (purple) for the crested eagle (red) and harpy eagle (blue) across environmental space from two principal components. Total variance explained by the two principal components = 73.34 % (PC1 = 45.81 %, PC2 = 27.53 %). Filled isopleths are kernel densities from 1-100%. Empty kernel density isopleths represent 1% density isopleth of the environment.

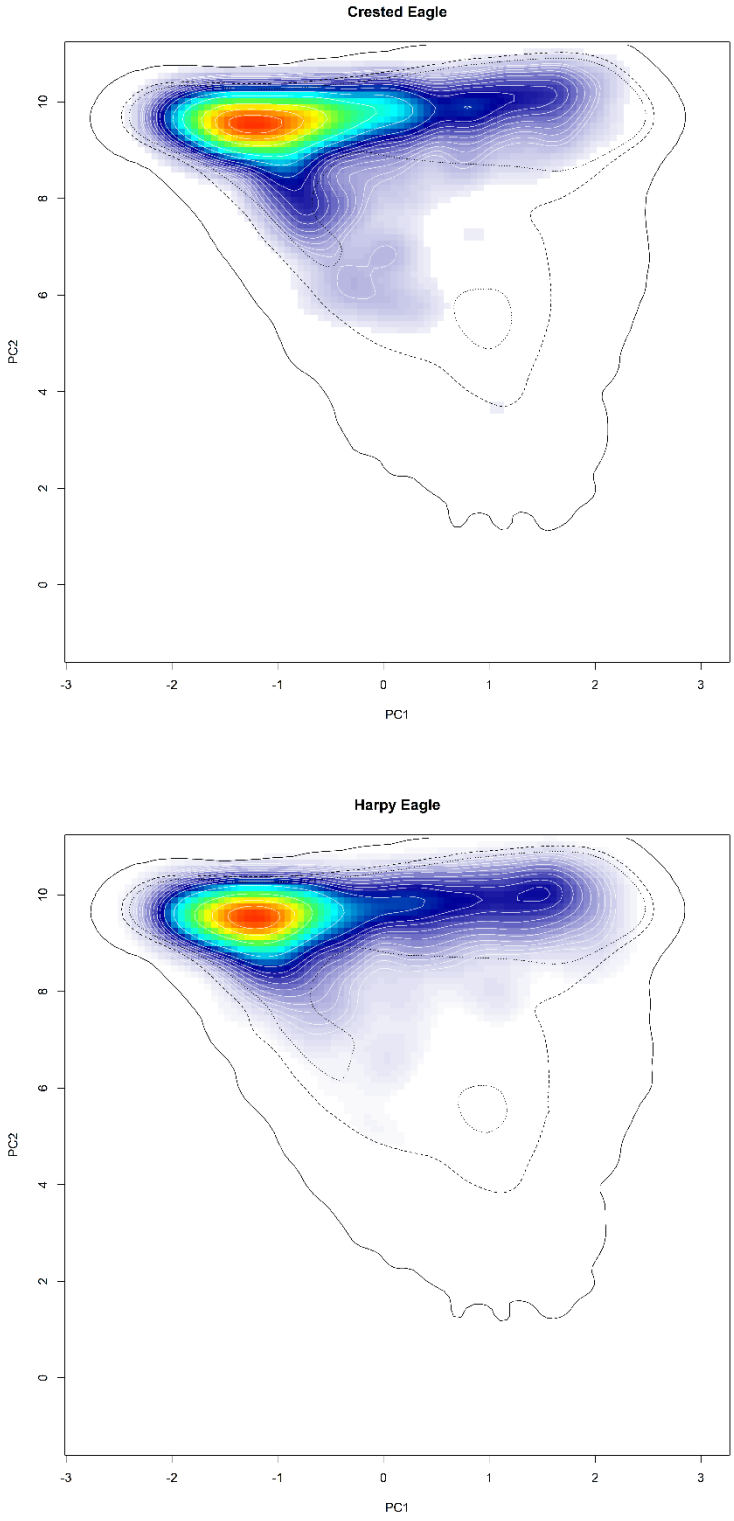


Figure 4.4. Distribution in environmental space for both eagles across two principal components. Red areas indicate highest environmental suitability. Filled kernel density isopleths characterize kernel density values from 0.4 (blue) to 0.99 (red). Black isopleth lines define kernel density of the corresponding environment, with black solid line = 0.1, black hashed line = 0.5, black dotted line = 0.75.

4.4.5 Habitat Suitability Model

The Harpiinae HSM had high calibration accuracy (mean CBI = 0.972), with the largest area of medium to high habitat across Amazonia and the Guiana Shield (Fig. 4.5). Medium to high areas of habitat were patchy across the largely deforested Atlantic Forest region in Brazil and Paraguay, but with a narrow corridor of habitat extending from part of the core range in Bolivia south into Jujuy and Salta provinces of northern Argentina. A further larger habitat corridor extended north from the Chocó-Darién ecoregion along the Pacific coast of Colombia, through Central America along the Caribbean coast. Habitat in the medium to high quantile classes (≥ 0.383) totalled ~9.2 million km^2, comprising 61 % of the total landscape area (Table 4.3). Medium to high core areas of habitat totalled ~3.5 million km^2, with core high habitat areas comprising 43 % of the total high habitat area. The largest continuous area of core high suitability habitat extended across the Guianan moist forest ecoregion into north-east Amazonia, along with the Chocó-Darién moist forest ecoregion in Colombia and Panama. Further high suitability habitat was identified in the moist forests adjacent to the east Andean slope, with patchy areas of high habitat in Misiones province in northern Argentina and the Serra do Mar coastal forests ecoregion in south-east Brazil.

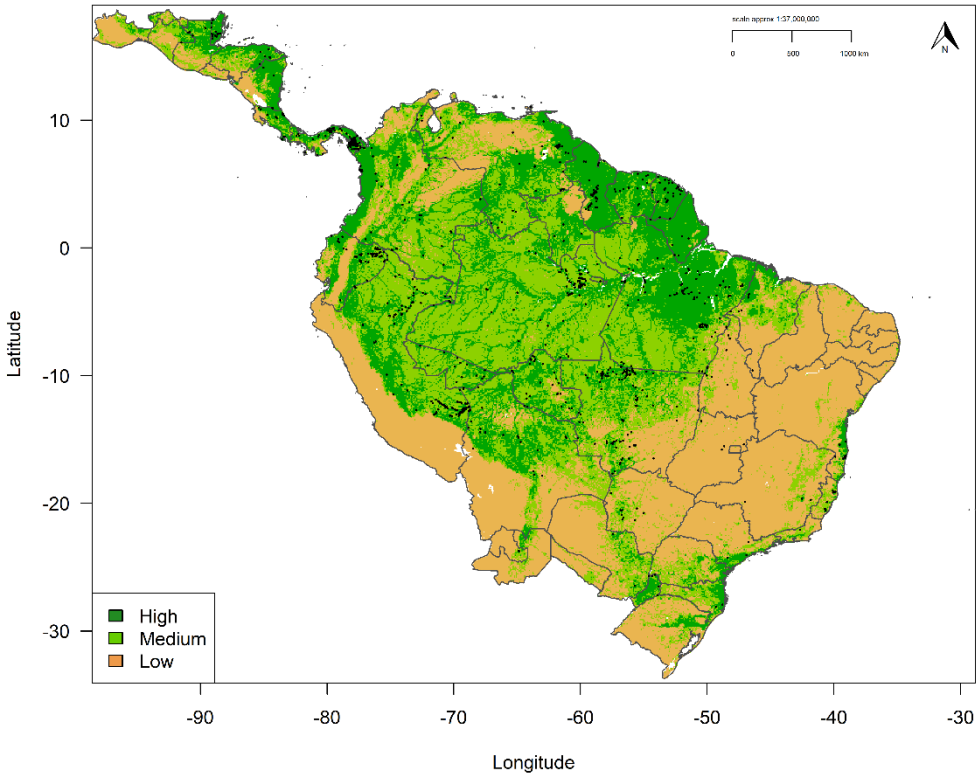


Figure 4.5. Habitat Suitability Model for Harpiinae eagles in Central and South America. Map denotes continuous GAM prediction reclassifed into three discrete quantile threshold classes (brown = low; pale green = medium; dark green = high). Grey borders define national boundaries and internal province and state boundaries for Argentina, Brazil, and Mexico. Black points define Harpiinae eagle occurrences.

Table 4.3. Class-level landscape metrics calculated from the reclassified Habitat Suitability Model quantile threshold classes. Values in parentheses are the proportions of each habitat class for each respective total habitat area and total habitat core area. Area values are in km^2.

Habitat class	Quantile threshold	Total area	Core area
High	>0.565	3,886,981 (0.26)	1,676,568 (0.11)
Medium	0.383-0.564	5,289,435 (0.35)	1,883,244 (0.13)
Low	<0.382	5,870,242 (0.39)	4,336,756 (0.29)
Total		15,046,658 (1.00)	7,896,568 (0.53)

4.5 Discussion

Previous localized studies on the co-occurrence of the crested and harpy eagle have produced contrasting results on the level of shared environmental space (Thiollay 1989; Sanaiotti *et al.* 2015). Here, I used a biogeographical perspective to identify environmental differences between these two eagles, knowing that factors affecting distribution in certain areas may not be generalizable into other regions within their shared range. Predictive GLMs identified narrow environmental niche breadth for both eagles, despite broad niche breadth measured in geographical space. Whilst resource overlap in geographical space was high using GLMs, there was only moderate niche overlap in environmental space using both GLMs and PCA-env. Both eagles shared identical environmental niches from randomization tests, with only subtle differences in distribution across environmental space. Thus, at the biogeographic scale both species can co-exist as long as there is sufficient habitat heterogeneity (Tilman 2004). The combined HSM identified the largest continuous areas of core Harpiinae habitat across the Guianan and Chocó-Darién moist forest ecoregions, along with moist lowland tropical forests adjacent to the east Andean slope.

4.5.1 Environmental differences

Most species are expected to be non-randomly distributed in environmental space and to occur within an optimal range of conditions (Hirzel *et al.* 2002). For the crested and harpy eagle, five and seven primary limiting factors respectively were sufficient to explain their distributions from the GLMs. Both distributions were negatively associated with areas of homogeneous vegetation, indicating a preference for areas of highly heterogenous vegetation. However, the harpy

eagle was more negatively associated with elevation and TRI compared to the crested eagle. This suggests that the harpy eagle is more restricted by topography than the crested eagle, though the reason for this difference is unclear. Perhaps nesting in emergent trees requires harpy eagles to select flatter, lower elevation areas where these tall trees are more common (Miranda *et al.* 2020; Vargas González *et al.* 2020). Further, both eagles had positive responses to increased evergreen forest cover (Fig. 4.2), but with the crested eagle less likely to be associated with this vegetation type than the harpy eagle (Table 4.2). Thus, the crested eagle may inhabit areas with lower evergreen forest cover, partly explaining how the two species co-exist - with crested eagles possibly able to persist into drier seasonal forest environments (Whitacre *et al.* 2012).

Although both eagles were most likely to be associated with areas of abundant evergreen forest, there were only slight differences in response to suitable landcover types. Both eagles had negative responses to mixed tree cover, but with the crested eagle more strongly negatively associated to them than the harpy eagle. Further, both the crested and harpy eagle had a somewhat broader tolerance to cultivated landcover than expected, though highest suitability was still for areas of ~20 % cultivated landcover. This suggests that both eagles may be able to adapt to more fragmented cultivated habitat, perhaps in the case of the harpy eagle taking ground-dwelling prey species in more open areas (Miranda 2015). Conversely, the crested eagle may be more reliant on mature forest, possibly associated with their stronger reliance on a diet of arboreal snakes and cavity nesting arboreal birds and mammals (Whitacre *et al.* 2012; Gomes *et al.* In press). Even so, this does not consider

how this may affect breeding performance, with harpy eagles having lower breeding productivity in fragmented habitats (Miranda *et al.* In review).

4.5.2 Resource overlap

Measuring the level of resource overlap in both geographical and environmental dimensions further revealed how both eagles respond to habitat conditions at different spatial resolutions. Measuring overlap in geographical space is relevant only for models estimating solely distribution. Whereas, measuring resource overlap in environmental space will often reveal the underlying processes determining the occupation of differing environmental space (Warren *et al.* 2019a). The results here support differences between geographical and environmental space, demonstrating the importance of measuring resource overlap across both geographic and environmental dimensions. Furthermore, altering the spatial resolution had little effect on the general pattern of moderate resource overlap. Importantly, both eagles had narrow niche breadth in environmental space when compared to geographic space, indicating habitat specialization. This follows the general observation for both eagles being generally reliant on highly speciose primary tropical forest (Whitacre *et al.* 2012; Miranda *et al.* 2019).

Using ordination to directly measure species-environment relationships at a coarser grain showed a similar moderate resource overlap to the fine-grain GLMs. Randomization tests showed no support for differing spatial niches, demonstrating that both eagles generally inhabit similar environmental spaces within the same geographical range. This follows the theory of niche conservatism, where the expectation is for greater niche equivalence between

pairs of sister-species (Wiens & Graham 2005; Warren *et al.* 2008). Niches can be conserved over long evolutionary timescales, with sister-species likely to inhabit similar environments, though not always identical (Wiens & Graham 2005). Given the high genetic similarity (~91 %) between these two eagle species (Lerner & Mindell 2005), the moderate resource overlap and equivalent niches supporting niche conservatism were expected. Thus, the results here show no support for competition restricting geographic range limits between either species, when regarding vegetation heterogeneity and topography. However, differing landcover use may be driven by the specific diet preferences of both eagles. Thus, any differences in habitat resource use may be occurring at a finer micro-habitat scale, which are undetectable at the continental geographic scale used here.

4.5.3 Habitat Suitability Model

Using spatial models calibrated with community science data is an effective method to estimate distribution (Bradter *et al.* 2017), despite issues of geographical sampling bias in such opportunistically collected datasets (Beck *et al.* 2014; Robinson *et al.* 2018). By aggregating occurrence data for both Harpiinae eagles, the high-resolution HSM was able to address under-sampling, identifying core habitat areas concentrated in the Chocó-Darién and Guianan moist forest ecoregions. However, the total area of medium to high habitat was consistent with previous range estimates for both Harpiinae eagles (Gomes & Sanaiotti 2015; Miranda *et al.* 2019). Systemically sampling species occurrence across large continental scales seems unrealistic because of the logistical difficulties of surveying across extensive and remote areas, such as Amazonia. Therefore, as demonstrated here, HSMs fitted to occurrence data above the

species-level may be a practical alternative for estimating range sizes for taxa that have broad distributions across remote areas (Qiao *et al.* 2017). By using modelling methods which are able to deal with inherent spatial biases, as outlined here, community science data can thus help fill distribution knowledge gaps in a convenient and cost-effective manner as first estimates of geographic range size.

4.5.4 Conclusion

Determining resource overlap between pairs of co-occurring species has long been a focus in ecology (Levins 1968; MacArthur 1972). Using spatial regression models and ordination has proven effective in this study for identifying resource overlap between these two tropical forest raptors. Both the crested and harpy eagle occupy equivalent environmental space within similar geographical ranges and show a moderate (but not significantly different) level of resource overlap. Because both eagles share the same environmental space, coexistence is perhaps driven by availability of each eagle's respective food resources. Habitat preference may be driven by where the most favourable food resources are distributed, perhaps accounting for the subtle differences in landcover preference within their shared range. The results here highlight the importance of measuring resource overlap using multiple grain resolutions, in both geographical and environmental dimensions to gain a broader view of the processes determining distribution for co-existing species with similar geographical ranges.

4.7 Appendices

Appendix 1 Supplementary Tables

Table S4.1. Multi-collinearity test using stepwise elimination Variance Inflation Factor (VIF) analysis for the GLMs. Variables with VIF < 10 have low correlation with other variables, and thus are suitable for inclusion in calibration models when further evaluated for ecological relevance.

Predictor	VIF
Evergreen Forest	4.41
Cultivated	2.54
Elevation	2.47
Mixed Trees	2.36
Terrain Roughness Index	1.78
Homogeneity	1.64

Appendix 2 Supplementary Figures

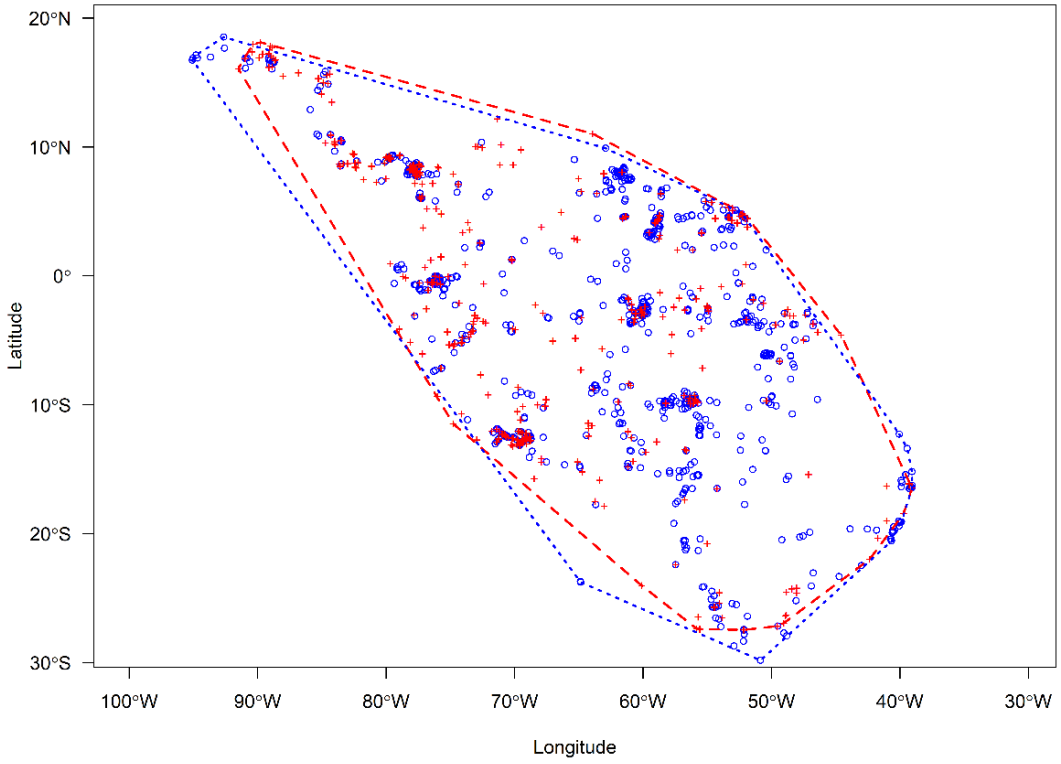
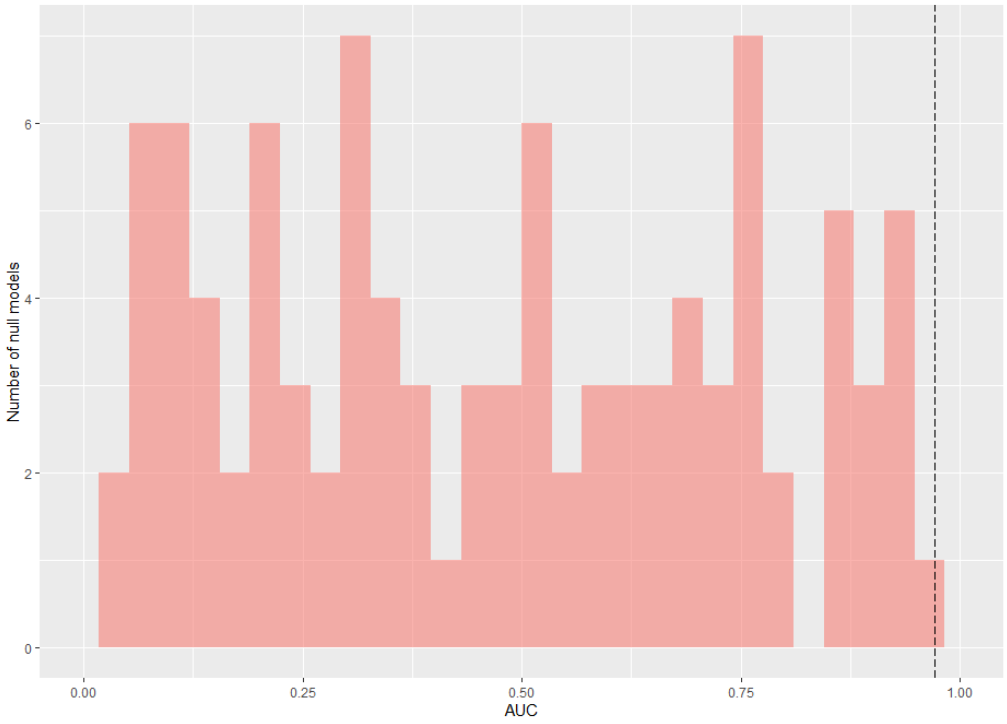


Figure S4.1. Unfiltered occurrences for the crested eagle (red crosses) and harpy eagle (blue circles) delimited in geographical space using convex hull models.

a.)



b.)

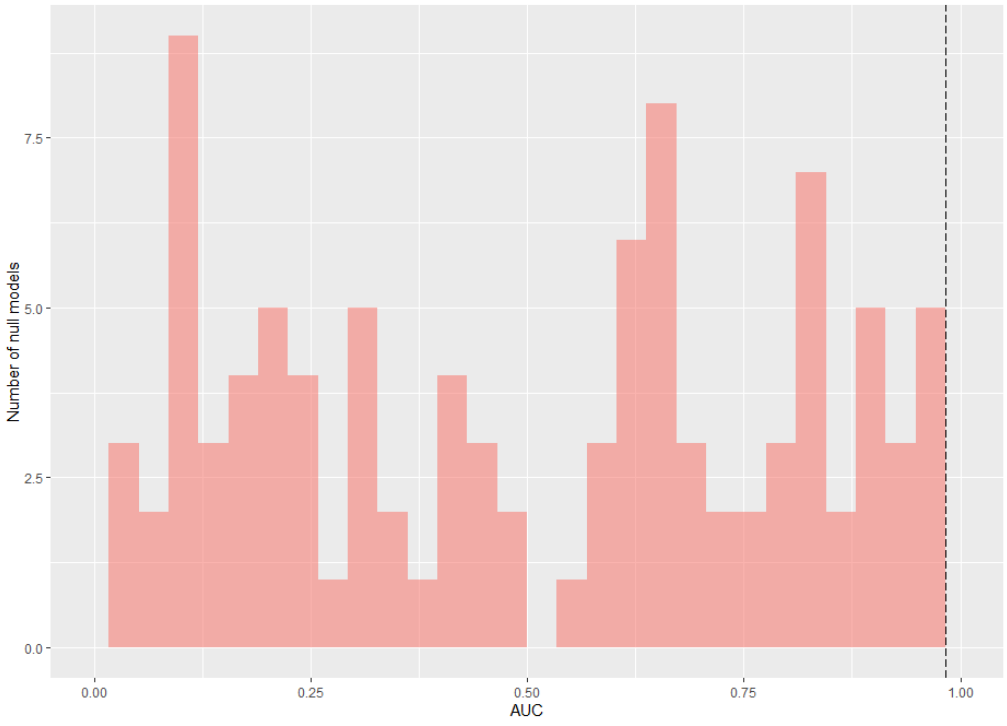


Figure S4.2. Monte-Carlo randomization test based on 100 random null models to test significance against best-fit model for the crested eagle (a) and harpy eagle (b) in environmental space. Dashed vertical line indicates AUC for each best fit model.

5. Range-wide habitat use and protected area coverage in a tropical forest raptor population across an increasingly deforested landscape.

5.1 Abstract

Quantifying habitat use is important for understanding how animals meet their requirements for survival and provides useful information for conservation planning. Currently, assessments of range-wide habitat use that limit species distributions at the population level are incomplete for many taxa. The harpy eagle (*Harpia harpyja*) is a large raptor of conservation concern, widely distributed across Neotropical lowland forests, that currently faces increasing threats from habitat loss and fragmentation. Here, I use a logistic regression modelling framework to identify habitat resource selection and predict habitat suitability based on the International Union for the Conservation of Nature (IUCN) Area of Habitat (AOH) concept. From the habitat use model, I performed a gap analysis to identify areas of high habitat suitability in regions with limited coverage in the Important Bird and Biodiversity Area (IBA) network. Range-wide habitat use indicated that harpy eagles prefer areas of 70-75 % evergreen forest cover, low elevation, and high vegetation heterogeneity. Conversely, harpy eagles avoid cultivated land, mosaic forest, and areas with complex topography. The habitat use model identified a large continuous area across the pan-Amazonia region, and a smaller habitat corridor from the Chocó-Darién ecoregion of Colombia running north along the Caribbean coast of Central America. Little or no habitat was predicted across the Atlantic Forest biome, which is severely degraded. The current IBA network covered ~17 % of medium to high suitability harpy eagle habitat exceeding the target representation (10 %). Four major gaps of unprotected high suitability habitat in the IBA network

were identified in the Chocó-Darién ecoregion of Colombia, north and west Guyana and north-west Brazil. I recommend these multiple gaps for harpy eagle habitat as new IBAs for strengthening the current IBA estate. Modelled area of habitat estimates as described here are a useful tool for large-scale conservation planning and can be readily applied to many taxa.

5.2 Introduction

Determining habitat resource use is a key aspect of wildlife ecology and conservation planning (Manly *et al.* 2002; Morrison *et al.* 2006). Understanding habitat use provides fundamental information about the nature of animals and how they meet their requirements for survival. Habitat use may proceed as a hierarchical process starting at broad spatial scales, down to fine-scale microhabitats (Johnson 1980; Boyce 2006). There is no single correct scale for studying wildlife-habitat relationships (Levin 1992), because animals view and react to their environment at various scales (Garshelis 2000). Most studies of habitat use are carried out at relatively small geographic scales or in specific habitat types (Morrison *et al.* 2006). Conversely, our understanding of species-habitat associations at the population-level across large continental extents is incomplete, even for well-studied groups such as birds (Gregory & Baillie 1998; Engler *et al.* 2017; Lees *et al.* 2020). Quantifying habitat use across the entire range of a population provides a comprehensive characterisation of habitat requirements, thus avoiding incomplete assessments of species-habitat relationships (Bellamy *et al.* 2020).

Many taxa face increasing threats from human-driven habitat loss and fragmentation across their entire range (Powers & Jetz 2019). Therefore,

developing a broad spatial approach to measuring habitat use is an effective starting point for conservation planning (Margules & Pressey 2000; Early *et al.* 2008). Identifying range-wide patterns in habitat use captures broad-scale processes, such as long-range dispersal, undetectable at smaller scales, which can then be used to direct and complement finer-scale assessments (Gregory & Baillie 1998; Morrison *et al.* 2006). Once habitat use is identified for a given species, those key variables can be used to infer a mapped representation of habitat across a focal species range (Hirzel *et al.* 2006). Habitat Suitability Models (HSMs), and related Resource Selection Functions (RSFs), are statistical methods that assess species' habitat requirements and predict distribution based on correlating environmental covariates with species occurrences (Boyce & McDonald 1999; Franklin 2009). Fitness should be higher in high quality habitat used more often, over other marginal habitat (Morrison *et al.* 2006). Once preferred habitat is identified, management actions can then be directed to guide conservation planning to protect or enhance those areas (Margules & Pressey 2000; Suárez-Seoane *et al.* 2002). Two example applications for HSMs are to re-evaluate range sizes (e.g., Herkt *et al.* 2017), and to identify gaps in protected area networks (e.g., de Carvalho *et al.* 2017).

Protected areas are a fundamental tool for conservation (Rodrigues & Cazalis 2020) and have been successful in reducing habitat loss and fragmentation for many taxa (Brooks *et al.* 2009; Geldmann *et al.* 2013). However, despite wide coverage in the global protected area network, gaps in protected area coverage still exist with new areas being continually added (Rodrigues *et al.* 2004a; Rodrigues *et al.* 2004b). Additionally, not all protected areas are located in areas deemed effective for conservation, but often designated by socio-

economic factors related to competing human activities (Pringle 2017; Morán-Ordóñez 2020; Rodrigues & Cazalis 2020). For birds, Important Bird and Biodiversity Areas (IBAs, BirdLife International 2019), are key sites of international significance for bird species which contain: (1) populations of globally threatened species, (2) populations and communities of range or biome restricted species, or (3) substantial congregations of bird species. IBAs also protect areas important for biodiversity and aim to overlap with the entire global protected area network (Donald *et al.* 2019). Indeed, the IBA concept has been the template for the development of Key Biodiversity Areas (KBAs; IUCN 2016), a logical evolution of IBAs which aim to identify and conserve sites of global importance to biodiversity (Donald *et al.* 2019).

Information on where to site IBAs can be used to identify where current protected area networks miss key bird species, and where these gaps need filling. Gap analysis is an established method to identify discontinuities in protected area networks (Scott *et al.* 1993) and has been effective in setting protected area priorities across a range of taxa (Margules & Pressey 2000). In particular, gap analysis has identified priority conservation areas for many taxa across the highly biodiverse Neotropics, for example odonate insects (Nóbrega & De Marco Jr. 2011), endemic birds and vertebrates (de Carvalho *et al.* 2017; Bax & Francesconi 2019), and a widely distributed raptor, the Andean condor (Perrig *et al.* 2020). The harpy eagle (*Harpia harpyja*) is a large raptor historically distributed throughout Neotropical lowland tropical forest from southern Mexico to northern Argentina (Miranda *et al.* 2019; Sutton *et al.* 2021), categorised as ‘Near-Threatened’ by the International Union for the Conservation of Nature (IUCN) due to continued habitat loss and persecution

(Birdlife International 2017). The species is now largely restricted to the tropical rainforest biome but can also inhabit dry seasonal forest and fragmented habitat (Vargas González *et al.* 2006; Silva *et al.* 2013).

Despite this habitat specialization, the harpy eagle has a large range due to the extensive distribution of lowland tropical forest across the Neotropical region. However, historical and ongoing deforestation has led to localized extinctions in parts of Central America and the Atlantic Forest of Brazil (Vargas González *et al.* 2006; Srbek-Araujo & Chiarello 2006; Silva *et al.* 2013; Meller & Guadagnin 2016). Current deforestation rates across the species' stronghold in Amazonia are also of significant conservation concern for its future persistence (Miranda *et al.* 2019). As an apex predator requiring large tracts of continuous tropical lowland forest for breeding and foraging (Vargas González *et al.* 2014; Miranda 2015), the harpy eagle may also act as a useful trigger species for designating new global IBAs (BirdLife International 2020). Further, as a Near-Threatened species of conservation concern it fulfils the criteria for designating new regional IBAs based on inferred habitat area (BirdLife International 2020).

Recently, the IUCN developed a new measure of range size termed Area of Habitat (AOH, Brooks *et al.* 2019). AOH is defined as the habitat available to a species based on habitat preferences and elevational limits within the mapped distributional range of a focal species. Various approaches have been taken to estimate AOH which all use a similar method of matching and overlaying the known mapped range, landcover and elevation limits of a given species (Brooks *et al.* 2019). Whilst the AOH method is useful and repeatable, it may still have limitations by missing areas that have no occurrence data but may still contain

preferred habitat. Indeed, HSMs can predict more complex and ecologically realistic geographic ranges compared to IUCN range maps (Breiner *et al.* 2017; Herkt *et al.* 2017). Using model-based interpolation based on the AOH guidelines but adapted to a correlative modelling approach (Da Silva *et al.* 2020), may be more effective for highlighting species-specific protected area gaps by identifying higher coverage of suitable pixels (Di Marco *et al.* 2017).

Drawing from these approaches, I develop predictive models here in a logistic regression framework, first using RSFs to identify preferred habitat, and second predicting habitat suitability in geographical space using an HSM. Estimating harpy eagle distribution based solely on habitat predictors at the continental scale should provide the most accurate and reliable estimate of range size due to the harpy eagle's generally high reliance on tropical lowland forest. Predicting habitat suitability across the known range can then be used to re-evaluate range size and assess the effectiveness of the IBA network. Specifically, I set out a baseline assessment of large-scale habitat use limiting harpy eagle distribution. A first estimate of modelled habitat suitability based on the Area of Habitat concept is then used to predict areas of highest habitat suitability for the harpy eagle. Using this information, I then generate a broad-scale gap analysis to identify priority areas of highest habitat suitability in regions with limited IBA network coverage. I aim to apply statistical modelling to systematic conservation planning to determine: **(1)** how effective the current IBA network is for covering areas of harpy eagle habitat, and **(2)** where gap areas of highest habitat suitability for the harpy eagle are located for inclusion as proposed IBAs.

5.3 Methods

5.3.1 Occurrence data

Harpy eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, The Peregrine Fund 2018), a data information system for all raptor species. For the harpy eagle, GRIN consists of occurrence data from the Global Biodiversity Information Facility (GBIF 2019a), which are mostly eBird records (79 %, Sullivan *et al.* 2009), along with two additional occurrence datasets (Vargas González & Vargas 2011; Miranda *et al.* 2019). Occurrences were cleaned by removing duplicate records, and those with no geo-referenced location. Only occurrences recorded from 2000 onwards were included to temporally match the timeframe of the habitat covariates. A 5 km spatial filter was applied between each occurrence point using the 'geoThin' function in the R package enmSdm (Smith 2019). Using a 5 km filter approximately matches the resolution of the raster data (~4.5-km) and reduces the effect of biased sampling (Kramer-Schadt *et al.* 2013). A total of 1021 geo-referenced records were compiled after data cleaning. Applying the 5 km spatial filter resulted in a filtered subset of 591 harpy eagle occurrence records for use in the calibration models.

5.3.2 Habitat covariates

To predict occurrence, habitat covariates representing topography, vegetation heterogeneity and landcover were downloaded from the EarthEnv (www.earthenv.org) and ENVIREM (Title & Bemmels 2018) databases. The EarthEnv database is a repository for global environmental data derived from satellite remote sensing, including vegetation heterogeneity and landcover layers. The ENVIREM dataset includes a set of two topographic covariates in

addition to EarthEnv. Covariates were selected *a prioiri* based on the IUCN AOH model criteria from landcover and topographic factors related empirically to harpy eagle distribution (Robinson 1994; Vargas González & Vargas 2011; Miranda *et al.* 2019; Sutton *et al.* 2021; Vargas González *et al.* 2020). A total of six continuous covariates (Table 5.1) were included at a spatial resolution of 2.5 arc-minutes (~4.5-km resolution). Raster layers were cropped using a delimited polygon consisting of all known range countries (including Formosa, Jujuy, Misiones and Salta provinces in northern Argentina, and Chiapas, Oaxaca, and Tabasco states in southern Mexico), further improving model predictive power by reducing the background area used for testing points in model evaluation (Radosavljevic & Anderson 2014).

Table 5.1. Habitat covariates used in all spatial modelling analyses for the harpy eagle.

Predictor	Source	Citation
Cultivated (%)	EarthEnv	Tuanmu & Jetz 2014
Elevation (m)	EarthEnv	Amatulli *et al.* 2018
Evergreen forest (%)	EarthEnv	Tuanmu & Jetz 2014
Homogeneity (0.0-1.0)	EarthEnv	Tuanmu & Jetz 2015
Mixed trees (%)	EarthEnv	Tuanmu & Jetz 2014
Terrain Ruggedness Index (TRI)	ENVIREM	Title & Bemmels 2018

Elevation and Terrain Roughness Index (TRI) are both key topographic variables determining harpy eagle distribution (Vargas González & Vargas 2011; Vargas González *et al.* 2020; Sutton *et al.* 2021). Elevation was derived from a digital elevation model (DEM) product from the 250 m Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010, Danielson & Gesch 2011). TRI was derived from the 30 arc-sec resolution Shuttle Radar Topographic Mission (SRTM30, Becker *et al.* 2009). Homogeneity is a similarity

measure for Enhanced Vegetation Index (EVI) between adjacent pixels; sourced from the Moderate Resolution Imaging Spectroradiometer (MODIS, https://modis.gsfc.nasa.gov/). Homogeneity varies between zero (zero similarity = maximum heterogeneity) and one (complete similarity). The three measures of percentage landcover (Evergreen Forest, Mixed Trees, Cultivated) are consensus products integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) at 30 arc-sec (~1km) spatial resolution. Mixed trees represents a mosaic landcover of forest, shrubland and grassland. All landcover layers were resampled to a spatial resolution of 2.5 arc-minutes using bilinear interpolation. Full details on methodology and image processing can be found in Tuanmu & Jetz (2014) for the landcover layers, and Tuanmu & Jetz (2015) for the habitat heterogeneity texture measures. All selected covariates showed low collinearity and thus all six were included as predictors in model calibration (Variance Inflation Factor (VIF) < 5; Table S5.1).

5.3.3 Modelling

5.3.1 Resource Selection Functions

An RSF between presence and the six covariates was fitted using logistic regression with a binomial error term and logit link using a generalised linear model (GLM) in the stats R package (R Core Team, 2018). The RSF followed geographical range first-order selection (Johnson 1980) using design I in a use-availability sampling protocol (Manly *et al.* 2002; Thomas & Taylor 2006). Linear and quadratic polynomial terms were fitted dependent on the scaled responses from fitting both terms on an initial model. Only linear terms were used when the quadratic term resulted in biologically unrealistic U-shaped curves, or when a linear term was sufficient to explain the scaled response. The RSF was fitted to

derive maximum likelihood estimates on model parameters significantly different from zero, with no interaction terms. Predictors were standardized with a mean of zero and standard deviation of one. Because the occurrence data correspond to a presence-only dataset, background availability (which plays the role of absences) was randomly sampled using 10,000 points suitable for regression-based modelling (Barbet-Massin *et al.* 2012), and equal weights assigned to both presence and background points. To test calibration accuracy the explained variance from each logistic model was measured using McFadden's adjusted R^2 (R^2_{adj}, McFadden 1974). Lastly, partial response curves based on the standardized covariates of the fitted model were plotted against the scaled responses with 95 % Confidence Intervals.

Ecological Niche Factor Analysis (ENFA, Hirzel *et al.* 2002; Basille *et al.* 2008) is a multivariate resource selection analysis extracting two measures of environmental space along two axes. The first axis metric, marginality (*M*), measures the position of the species' ecological niche, and its departure relative to the available environment. A value of M >1 indicates that the niche deviates more relative to the reference environmental background and has specific environmental preferences compared to the available environment. The second axis metric, specialization (*S*), is an indication of niche breadth size relative to the environmental background, with a value of S >1 indicating higher niche specialization (narrower niche breadth). A high specialization value indicates a high reliance on the environmental conditions that mainly explain that specific dimension. ENFA was carried out in the R package CENFA (Rinnan 2018), weighting all cells by the number of observations (Rinnan & Lawler 2019). Predictors were rescaled thus the ENFA can be interpreted similar to a PCA

with eigenvalues and loadings represented along the first axis of marginality and the following secondary orthogonal axes of specialization (Basille *et al.* 2008).

5.3.2 Habitat Suitability Model

HSMs were fitted using penalized elastic-net logistic regression (Zou & Hastie 2005; Fithian & Hastie 2013), in the R packages glmnet (Friedman *et al.* 2010) and maxnet (Phillips *et al.* 2017). Elastic net logistic regression imposes a penalty (known as regularization) to the model shrinking the coefficients of variables that contribute the least towards zero (or exactly zero), to reduce model complexity (Gastón & García-Viñas 2011; Helmstetter *et al.* 2020). The maxnet package is based on the maximum entropy (MAXENT; Phillips *et al.* 2017) algorithm, equivalent to an inhomogeneous Poisson process (IPP; Fithian & Hastie 2013; Renner & Warton 2013; Renner *et al.* 2015). In its original implementation MAXENT imposed a 'lasso' (least absolute shrinkage and selection operator) regularization penalty, where only the most significant variables are kept in the model, with uninformative variables set at zero. Conversely, the maxnet package uses an elastic net to perform automatic variable selection and continuous shrinkage simultaneously (Zou & Hastie 2005; Phillips *et al.* 2017), retaining all variables that contribute less by shrinking coefficients to either exactly zero or close to zero. Elastic net regularization outperforms predictive accuracy compared to the lasso, in both simulated and real data examples (Zou & Hastie 2005) and may be viewed as a generalization of the lasso.

Within the maxnet package the complementary log-log (cloglog) transform was selected as a continuous index of environmental suitability, with 0 = low suitability and 1 = high suitability. Phillips *et al.* (2017) demonstrated the cloglog transform is equivalent to an IPP and can be interpreted as a measure of relative occurrence probability proportional to a species potential abundance. A random sample of 10,000 background points were used as pseudo-absences recommended for regression-based modelling (Barbet-Massin *et al.* 2012) and to sufficiently sample the background calibration environment (Guevara *et al.* 2018). Optimal-model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989), to determine the most parsimonious model from two key MAXENT parameters: regularization multiplier (β) and feature classes (Warren & Seifert 2011). Eighteen candidate models of varying complexity were built by comparing a range of regularization multipliers from 1 to 5 in 0.5 increments, and two feature classes (response functions: Linear, Quadratic) in all possible combinations using the 'trainMaxNet' function in the R package enmSdm (Smith 2019). All models with a $\Delta AIC_c < 2$ were considered as having strong support (Burnham & Anderson 2004), and the model with the lowest β selected to avoid model overfitting. Response curves and parameter estimates were used to measure variable performance within the optimal calibration model.

Continuous Boyce index (CBI; Hirzel *et al.* 2006) was used as a threshold-independent measure of how predictions differ from a random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent with a Spearman correlation (r_s) with CBI values ranging from -1 to +1, with positive values indicating predictions consistent with observed presences, values close to zero

no different than a random model, and negative values indicating areas with frequent presences having low environmental suitability. Mean CBI was calculated using five-fold cross-validation on 20 % test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019). The optimal model was tested against random expectations using partial Receiver Operating Characteristic ratios (pROC), which estimate model performance by giving precedence to omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios range from 0 – 2 with 1 indicating a random model. Function parameters were set with a 10% omission error rate, and 1000 bootstrap replicates on 50% test data to determine significant ($\alpha = 0.05$) pROC values >1.0 in the R package ENMGadgets (Barve & Barve, 2013).

5.3.4 Gap analysis

To calculate Area of Habitat in suitable pixels and assess the effectiveness of the IBA network, the continuous prediction was reclassified to a binary threshold prediction. All pixels equal to or greater than the median pixel value of 0.345 from the continuous model were used as a suitable threshold for conservation planning (Liu *et al.* 2005; Rodríguez-Soto *et al.* 2011; Portugal *et al.* 2019), with the resulting binary map consistent with current knowledge on harpy eagle distribution (Miranda *et al.* 2019). The IBA network polygons (as of September 2019; BirdLife International 2019) were then clipped to the reclassified area, establishing those IBAs covering pixels of habitat suitability ≥ 0.345 threshold. To visualise IBA network coverage, the continuous prediction was then reclassified into four discrete quantile suitability classes (No habitat: 0.0 - 0.067; Low: 0.068 - 0.344; Medium: 0.345 - 0.701; High: 0.702 - 1.000).

The clipped IBA network polygons were then overlaid onto the discrete class map identifying those pixels of medium to high habitat suitability ≥ 0.345 threshold which were within the clipped IBA network polygons. The threshold range size was then used to calculate a protected area 'representation target', quantifying how much protected area representation is needed for a species dependent on its range size following the formulation of Rodrigues *et al.* (2004a),

$$\text{Target} = \max(0.1, \min(1, -0.375 \times \log10(\text{range size}) + 2.126))$$

where 'Target' is equal to the percentage of protected target representation required for the species 'range size', as used in subsequent applications of the formula (Butchart *et al.* 2015; Di Marco *et al.* 2017). As can be verified by inserting different range size values, this formula yields a target of 10 % for species with a range size >250,000 km^2 and increasing proportional representation for smaller range sizes up to a target of 100 % if range size <1000 km^2. Current IBA coverage was used to calculate the difference between the current level of IBA coverage compared to the target level representation. General model development and geospatial analysis were performed in R (v3.5.1; R Core Team, 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017), rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundle 2019) and sp (Bivand *et al.* 2013) packages.

5.4 Results

5.4.1 Resource Selection Functions

The GLM was able to explain 87 % of the variability in habitat use (McFadden's R^2_{adj} = 0.87). Six predictors had significant terms (Table 5.2), with the harpy eagle most likely to be positively associated with the proportion of evergreen forest, and less likely to be associated, in declining order, with higher elevation, homogeneity, and proportion of cultivated land. Increasing elevation had the strongest negative association, followed by homogenous vegetation and cultivated areas (Fig. 5.1).

Table 5.2. Linear and Quadratic (defined with superscript 2) terms derived from maximum likelihood estimates obtained from the full model with 95 % Confidence Intervals. Covariates ranked by the value of the regression coefficient estimates

Predictor	Estimate	Lower CI	Higher CI	*z*	*p*
Intercept	-0.86	-1.01	-0.70	-10.65	0.001
Evergreen Forest	115.33	89.08	141.58	8.61	0.001
Elevation	-106.11	-139.90	-72.32	-6.16	0.001
Homogeneity	-86.84	-101.07	-72.61	-11.96	0.001
Cultivated^2	-57.49	-76.45	-38.53	-5.94	0.001
Cultivated	-33.20	-58.73	-7.67	-2.55	0.042
Mixed Trees	-28.84	-50.67	-7.01	-2.59	0.062
Terrain Roughness Index^2	-27.79	-51.38	-4.21	-2.31	0.017
Mixed Trees^2	7.62	-8.74	23.98	0.91	0.478
Terrain Roughness Index	0.26	-25.27	25.79	0.02	0.987

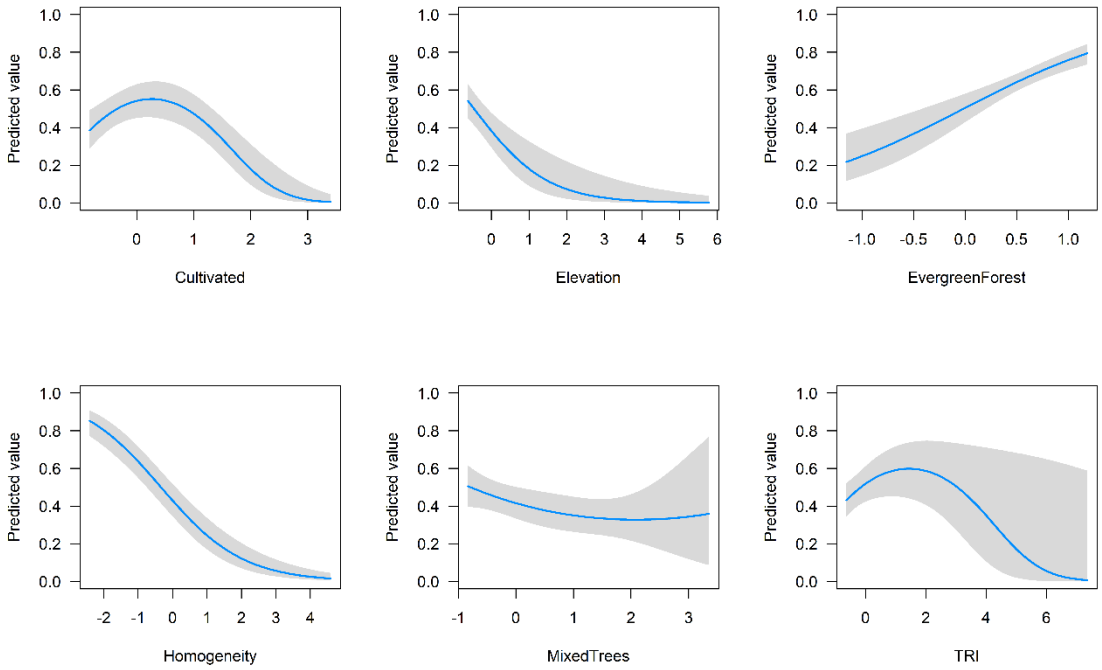


Figure 5.1. Scaled partial response curves with 95 % Confidence Intervals (grey shading) derived from maximum likelihood estimates obtained from the RSF. X-axis values are the standardized responses for each covariate (mean = 0, variance = 1). TRI = Terrain Roughness Index.

The ENFA habitat space deviated from the average background habitat available (Fig. 5.2), with the marginality factor higher than the available background habitat (*M* = 1.026). The harpy eagle is restricted to specific habitat relative to the background habitat with specialized habitat requirements (*S* = 1.886). Four significant ENFA factors explained 86.19 % of total variance, with the first specialization axis (Spec1) explaining 43.78 % (Table S5.2). Evergreen forest had the highest coefficient on the marginality axis (0.69), and elevation the highest on the specialization axis (0.89).

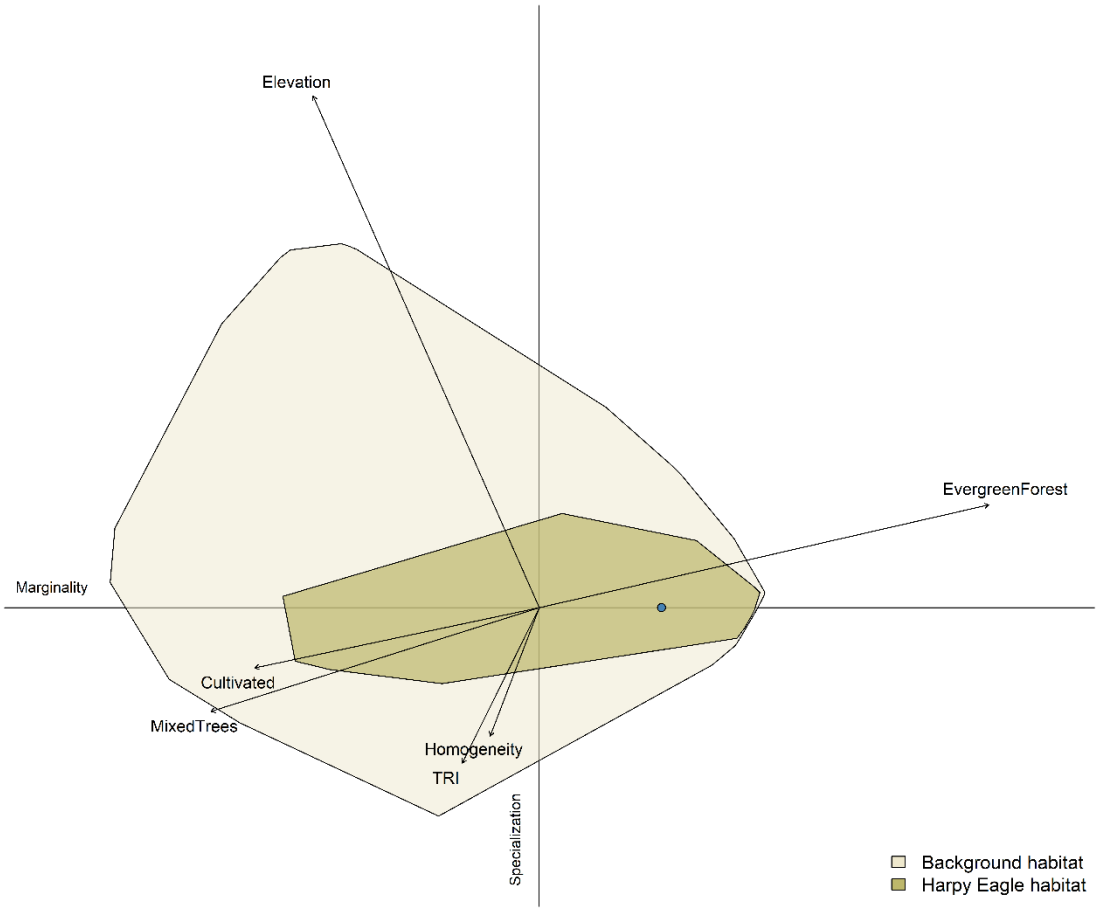


Figure 5.2. Ecological Niche Factor Analysis (ENFA) for suitable harpy eagle habitat space (khaki) within the available background environment (beige) shown across the marginality (x) and specialization (y) axes. Arrow length indicates the magnitude with which each variable accounts for the variance on each of the two axes. Blue point indicates niche position (median marginality) relative to the average background environment (the plot origin).

5.4.2 Habitat Suitability Model

Six candidate models had an $\Delta AIC_c \leq 2$, and the model with the lowest regularization multiplier (β) selected (Table S5.3). The best-fit HSM (ΔAIC_c = 1.19) had response parameters Linear and Quadratic and β = 2.5, with high calibration accuracy (mean CBI = 0.960), and was robust against random expectations (pROC = 1.431, SD± 0.055, range: 1.244 – 1.594). Harpy eagles were most positively associated with evergreen forest and negatively associated with habitat homogeneity (Table 5.3). The largest continuous area of habitat extended across Amazonia and the Guiana Shield (Fig. 5.3). A habitat corridor was identified through Central America along the Caribbean coast, extending south into the Chocó-Darién ecoregion along the Pacific coast of Colombia. Little or no habitat was predicted across the largely deforested Atlantic Forest region in Brazil. From the HSM response curves, evergreen forest had peak suitability at 70-75 % forest cover, with highest suitability for topographic areas of both low elevation and terrain ruggedness (Fig. 5.4). Habitat suitability was highest in areas of low homogeneity < 0.2 (i.e. highly heterogenous vegetation), and areas with zero or low percentage cover of mixed trees (i.e. mosaic forest and shrub/grassland) and human cultivated land.

Table 5.3. Parameter estimates derived from the HSM penalized elastic net regression beta coefficients.

Predictor	Linear	Quadratic
Homogeneity	-3.85	
Evergreen Forest	0.07	0.00
Mixed Trees	-0.03	
Terrain Roughness Index	-0.02	
Cultivated	-0.01	0.00
Elevation	0.00	

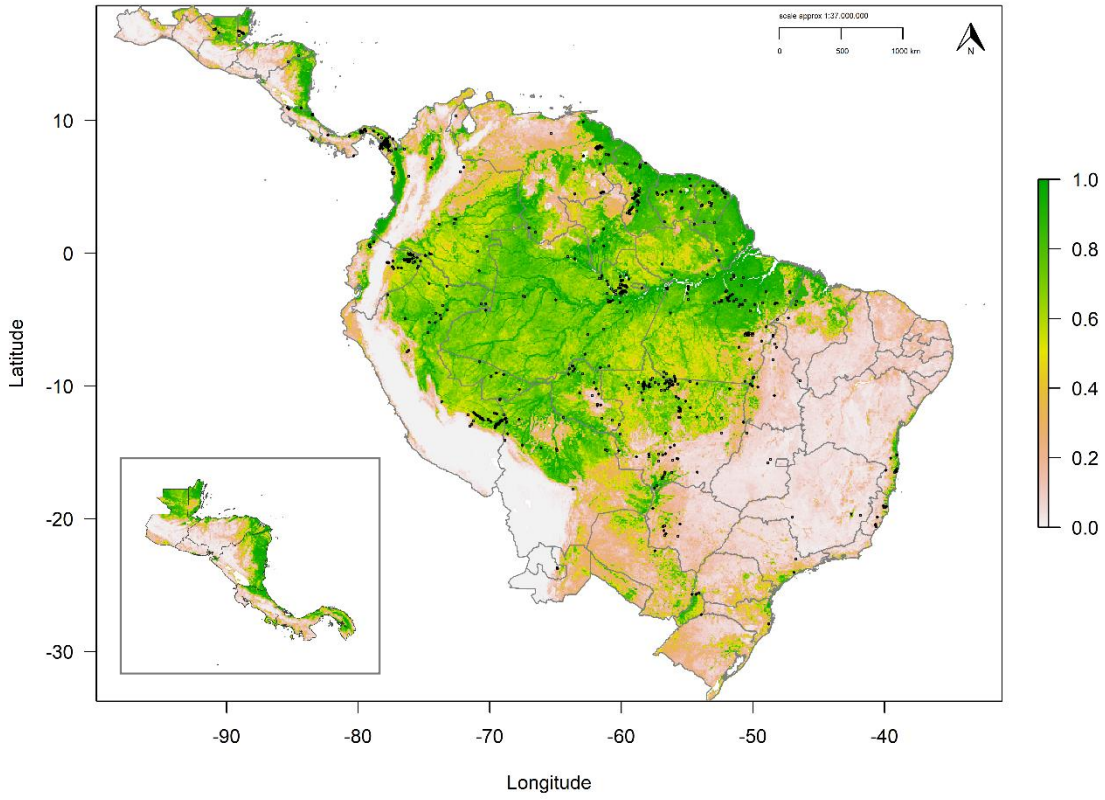


Figure 5.3. Habitat Suitability Model for the harpy eagle. Map denotes cloglog prediction with darker green areas (values closer to 1) having highest suitability and expected abundance. Grey borders define national boundaries and internal state boundaries for Argentina, Brazil, and Mexico. Black points define harpy eagle occurrences. Inset map shows cropped model prediction for Central America without harpy eagle occurrences for clarity.

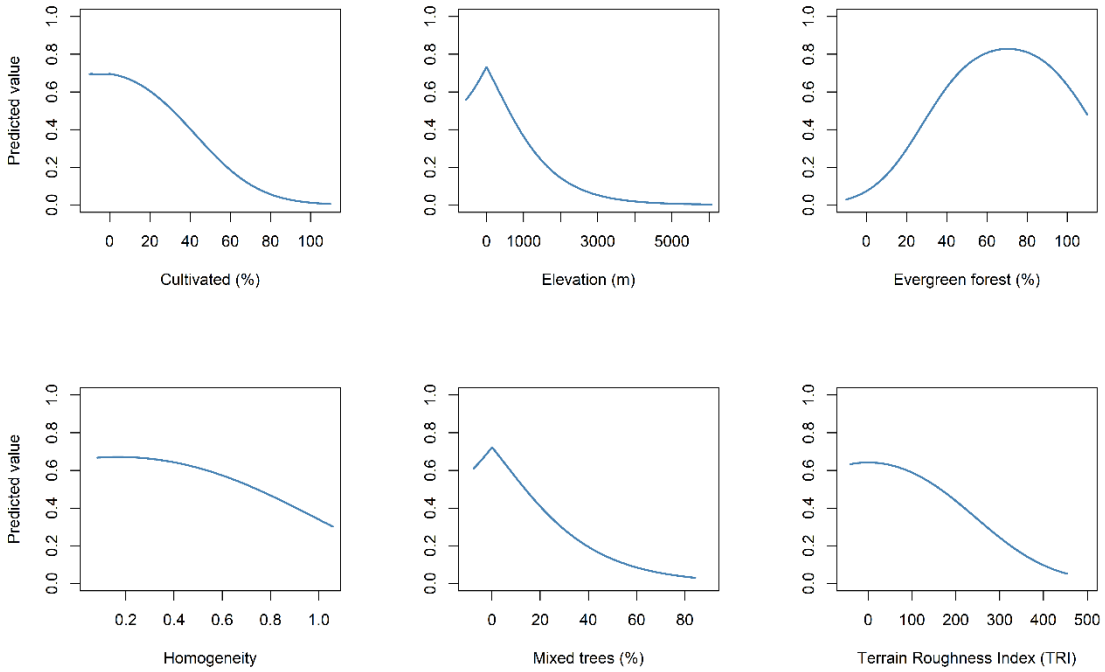


Figure 5.4. Predictor response curves from the Habitat Suitability Model for the harpy eagle.

5.4.3 Range size and gap analysis

The reclassified binary model (median threshold = 0.345) calculated an Area of Habitat equalling 7,566,339 km^2 (Fig. S5.1). The current IBA network covered 16.9 % (1,275,917 km^2), of this habitat area in the medium to high discrete quantile classes (Fig. 5.5), 6.9 % greater than the target representation (10 %). Four major gaps (Fig. 5.5, hashed blue ellipses) for high threshold habitat without extensive IBA coverage were identified in: (**1**) the Chocó-Darién ecoregion in western Colombia (Fig. 5.6), (**2**) the Magdalena-Urabá moist forests of northern Colombia (Fig. 5.6), (**3**) north-east Amazonas state in Brazil and (**4**) north and west Guyana.

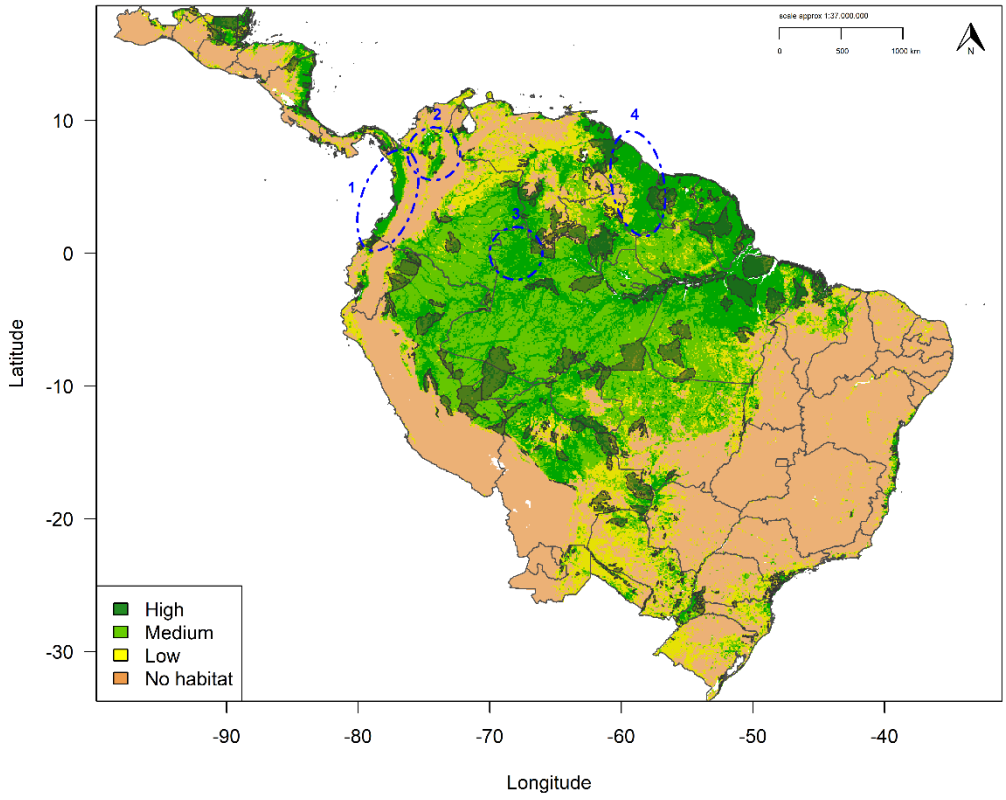


Figure 5.5. Important Bird and Biodiversity Area (IBA) network gap analysis for harpy eagle habitat. Map denotes cloglog prediction reclassifed into four discrete quantile threshold classes (brown = no habitat; yellow = low, pale green = medium; dark green = high). Black bordered polygons denote current IBA network. Hashed blue ellipses identify priority IBA network coverage gaps: (**1**) Chocó-Darién region in Colombia, (**2**) Magdalena-Urabá moist forests in northern Colombia, (**3**) north-east Amazonas state in Brazil, (**4**) north and west Guyana. Grey borders define national boundaries and internal province and state boundaries for Argentina, Brazil, and Mexico.

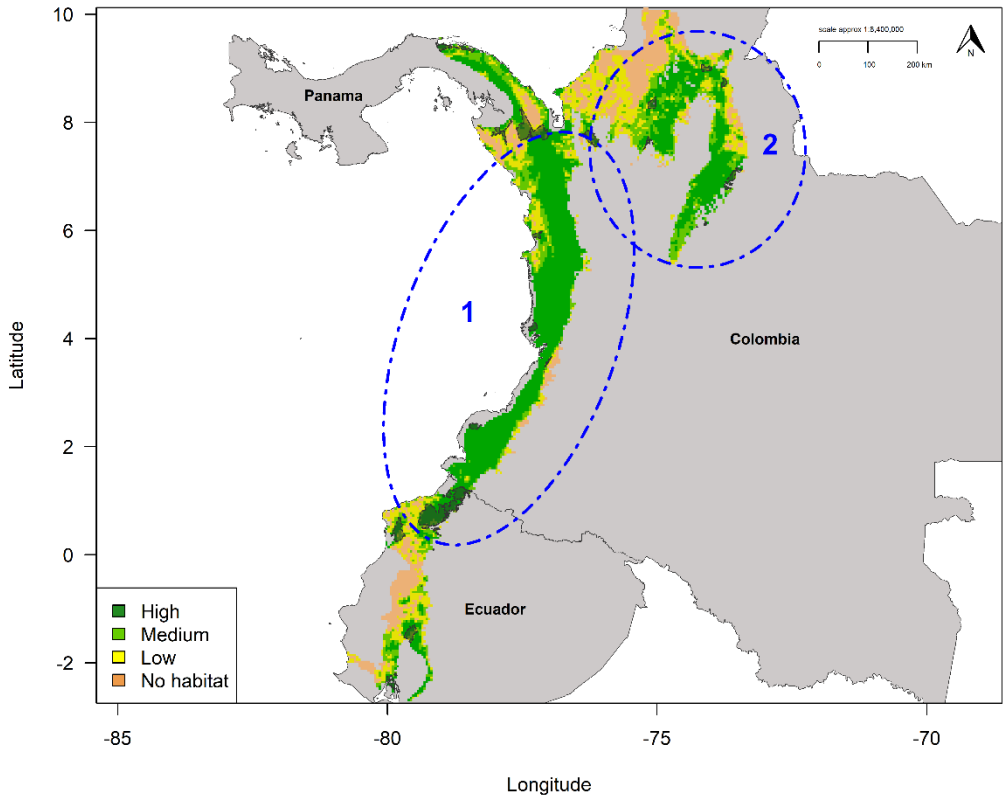


Figure 5.6. Important Bird and Biodiversity Area (IBA) network gap analysis for harpy eagle habitat projected into the Chocó-Darién ecoregion. Map denotes cloglog prediction reclassifed into four discrete quantile threshold classes (brown = no habitat; yellow = low, pale green = medium; dark green = high). Black bordered transparent polygons denote current IBA network. Hashed blue ellipses identify priority IBA network coverage gaps: (**1**) Chocó-Darién region in Colombia and Panama, (**2**) Magdalena-Urabá moist forests in northern Colombia.

5.5 Discussion

The results indicate that viable harpy eagle populations are more likely to be associated with 70-75 % evergreen forest cover, lower elevation, and high vegetation heterogeneity across their range. Conversely, harpy eagles seem to avoid areas of cultivated land, mosaic forest, and high terrain complexity. Using the AOH parameters as a basis for a habitat model predicted a large area of habitat across the pan-Amazonia region, and a habitat corridor extending from the Pacific coast of Colombia, north along the Caribbean coast of Central America. Almost no habitat was predicted across the Atlantic Forest region. The current IBA network coverage exceeded the target representation (10 %), covering ~17 % of medium to high harpy eagle habitat. Considering the large range of the harpy eagle, the current IBA extent is encouraging but misses key areas of potentially important habitat. Four major habitat gaps in the IBA network were identified in north and west Colombia, Guyana and north-west Brazil (Fig. 5.5). I recommend establishing new IBAs in these four gap areas, further strengthening the current IBA network across the region.

5.5.1 Habitat use

Broad and fine scale species-habitat assessments often result in different variables emerging as important, thus having contrasting implications for conservation (Gregory & Baillie 1998). However, the models here show general similarities to habitat models from previous studies at both broad and fine scales. The HSM was consistent with predicted harpy eagle habitat from a previous broad-scale HSM (Miranda *et al.* 2019). This was expected because both HSMs used measures of forest cover as landcover predictors but with differing modelling methodologies. This reinforces the consistency in HSM

outputs for the harpy eagle from a range of algorithms and gives confidence in HSM predictions which have been criticised for lacking ecological realism (Fourcade *et al.* 2017). Building on the Miranda *et al.* model, the HSM here also predicted a distinct corridor of habitat extending from the Chocó-Darién ecoregion of west Colombia north through Central America along the Caribbean coast (Fig. 5.6). This suggests the select number of topographic and landcover predictors used here were able to identify key areas of habitat undetectable from other texture measures used in a previous HSM for the harpy eagle (Miranda *et al.* 2019).

The HSM confirmed the restricted elevational distribution for the harpy eagle, consistent with a landscape-level HSM from Panama (Vargas González *et al.* 2020). This may be linked to both a preference for nesting in large, canopy-emergent trees, and the abundance of the harpy eagles' main prey of large, arboreal mammals, both of which are found in greater abundance at lower elevations (see Chapter 3; Miranda 2015; Miranda *et al.* 2020; Vargas González *et al.* 2020). Harpy eagles are dependent on large tracts of lowland tropical forest for breeding and foraging (Vargas González *et al.* 2014; Miranda 2015; Miranda *et al.* 2019). Indeed, breeding success was higher in areas with > 70 % forest cover in northern Mato Grosso, Brazil (Miranda *et al.* In review), consistent with the range-wide response to evergreen forest cover here. Perhaps as important, strong negative associations were identified with human cultivated land and mosaic forest, showing that harpy eagles avoid both these human-induced landcover types. This implies that, as deforestation increases across the species' range, the harpy eagle may struggle to adapt to disturbed, fragmented landscapes (Miranda *et al.* In review).

5.5.2 Area of Habitat

The Area of Habitat estimate refines previous range size estimates (Birdlife International 2017; Sutton *et al.* 2021) and provides a more realistic distributional area for the harpy eagle. There was 31.6 % less area in the modelled AOH range polygon (7,566,339 km^2), compared to the current IUCN range map polygon (11,064,295 km^2), and 23 % less area in the modelled AOH polygon when compared to an HSM using solely climatic and topographic predictors (9,844,399 km^2; Sutton *et al.* 2021). Therefore, I recommend this new estimate be incorporated into future IUCN assessments for the species.

One limitation of the analyses was the timeframe of the remote-sensing data used for the predictors. Both the landcover and vegetation data used here are a consensus product collected between the years 2000-2005, and it is reasonable to assume land use has changed considerably since then (Powers & Jetz 2019). Therefore, the area of habitat prediction should be viewed as a baseline assessment, knowing that landcover can change rapidly. However, processing large areas of current remote-sensed landcover data at continental-scales can be problematic due to the high computing power required. Even so, the EarthEnv dataset used is recommended as a readily available dataset of habitat variables to use for first estimates of modelled AOH at large scales (Tuanmu & Jetz 2014, 2015).

Current and predicted future habitat loss may lead inevitability to declines in populations of some species, increasing their extinction risk (Powers & Jetz 2019). Continued habitat loss and fragmentation is likely to have a negative

impact on the future persistence for many birds across the highly biodiverse Neotropics (Bird *et al.* 2011). The harpy eagle is a good example, despite its large range precluding high extinction risk (Gaston & Fuller 2009). Continued habitat loss and fragmentation through agricultural development and logging across its geographic range (Miranda *et al.* 2020; Vargas González *et al.* 2006) should raise the alarm about the species' future conservation status (Krüger & Radford 2008; Miranda *et al.* 2019). This is demonstrated by the few harpy eagle breeding and sighting records in the largely deforested Atlantic Forest (Srbek-Araujo & Chiarello 2006; Meller & Guadagnin 2016), and parts of Central America (Vargas González *et al.* 2006), which is reflected in the results from the HSM presented here. The results should therefore serve as a fore-warning of what could happen across parts of the core habitat area in Amazonia where deforestation has steadily increased since 2000 (Hansen *et al.* 2008).

As a baseline assessment, the HSM should be viewed as a maximum extent of habitat, knowing that deforestation is still ongoing across the pan-Amazonia region (Bird *et al.* 2011; Hansen *et al.* 2020). Approximately 18 % of tropical forest in Amazonia had been cleared by 2011 (Bird *et al.* 2011), with predictions of up to 40 % of forest cover lost by 2050 based on extrapolating planned infrastructure developments across the region (Soares-Filho *et al.* 2006). Recently, those tropical forests of highest structural integrity most associated with preferred harpy eagle habitat (tall, closed canopy forest and low human pressure; Vargas González *et al.* 2014; Miranda *et al.* 2020), were identified as largely limited to the Amazon basin (Hansen *et al.* 2020). However, these forests generally remain intact due to their remoteness (Soares-Filho *et al.* 2006), but with the majority having no formal protection. Therefore,

strengthening protected area networks should be given high priority in policy decisions (Butchart *et al.* 2015), along with effective area-based conservation outside of, but concurrent with, formally protected areas (Pringle 2017; Maxwell *et al.* 2020).

5.5.3 Gap analysis

The current coverage of the IBA network within the modelled AOH range (~17 %) exceeded the representative target set here (10 %). However, it is still somewhat lower than the proportion of IBA network coverage for threatened bird species overall in Amazonia (54.9 %, Bird *et al.* 2011). Of the four key gaps identified here only gap 3 in north-west Amazonas state in Brazil has any form of current protection as an area of indigenous land (UNEP-WCWC 2020). The three remaining gap areas have little formal protection or IBA coverage, despite both the Chocó-Darién ecoregion (gap 1) and Guyana (gap 4) having extensive harpy eagle habitat. In the case of north and west Guyana it is likely that most habitat is 'passively' protected due to the inaccessibility of the region. However, solely relying on remoteness may be short-sighted and extending the current IBAs east and west of Guyana to cover a larger portion of the Guiana Shield is recommended.

The Chocó-Darién ecoregion is one of 25 global biodiversity hotspots prioritized for conservation measures (Myers *et al.* 2000). Based on remote sensing satellite imagery, deforestation rates have steadily increased in the region over the past two decades driven by agricultural expansion (Fagua *et al.* 2019; Fagua & Ramsey 2019). Approximately 42 % of forest remains intact, making this an area of high importance for protection not only for the harpy eagle but for

all the associated fauna and flora. Establishing and reinforcing the current IBA network throughout the Chocó-Darién ecoregion could be important for habitat continuity essential to dispersing harpy eagles (Urios *et al.* 2017) between Central and South America. The Darién region of Panama has a high density of breeding harpy eagles (Vargas González & Vargas 2011) and is considered the current stronghold of the species in Central America. Designating new IBAs in the Chocó-Darién ecoregion corridor could thus protect habitat for fragmented harpy eagle populations maintaining genetic diversity and thus potential adaptation to environmental change (Lerner *et al.* 2009; Banhos *et al.* 2016; Maxwell *et al.* 2020). Indeed, genetic diversity decreased in fragmented harpy eagle populations inhabiting deforested regions of the southern Amazon and Atlantic Forest of Brazil (Banhos *et al.* 2016), reinforcing the need to protect and link habitat patches throughout the harpy eagle's entire distribution.

5.5.5 Conclusion

Habitat loss is a principal threat to the long-term survival of the harpy eagle and protecting as much of the remaining tropical forest habitat for the species should be a high priority (Banhos *et al.* 2016). Using targeted forest protection through responsible community land use and broad-scale conservation planning is needed to reduce current deforestation rates (Kramer *et al.* 1997; Bird *et al.* 2011; Butchart *et al.* 2015). Across their range harpy eagles prefer evergreen forest cover between 70-75 %, which should be used as a threshold target for conserving habitat. Whilst the current IBA network coverage for the harpy eagle exceeded the representation target, the models here identified gaps in the IBA network that ought to be prioritised for enlarging the IBA network estate. As demonstrated here, modelled area of habitat estimates based on HSMs are a

useful tool for large-scale conservation planning and can be readily applied to many taxa.

5.7 Appendices

Appendix 1 Supplementary Tables

Table S5.1. Multi-collinearity test using stepwise elimination Variance Inflation Factor (VIF) analysis. Variables with VIF < 5 have low correlation with other variables, and thus are suitable for inclusion in calibration models when further evaluated for ecological relevance.

Predictor	VIF
Homogeneity	1.65
Terrain Ruggedness Index	1.76
Elevation	2.41
Mixed trees	2.54
Cultivated	2.62
Evergreen forest	4.64

Table S5.2. Variance explained by the four most significant ENFA factors (Marg. = marginality; Spec = Specialization) and coefficient values (eigenvectors) ordered from highest to lowest on the marginality factor.

ENFA axis	Marg.	Spec1	Spec2	Spec3
Variance explained (%)	11.37	43.78	18.01	13.03
Predictor				
Evergreen forest	0.69	0.18	-0.62	0.56
Mixed trees	-0.50	-0.18	-0.14	0.72
Cultivated	-0.43	-0.11	-0.65	-0.13
Elevation	-0.35	0.89	-0.32	0.31
Terrain Roughness Index	-0.12	-0.27	0.19	-0.17
Homogeneity	-0.08	-0.22	0.18	-0.13

Table S5.3. Model selection metrics for all six candidate models with $\Delta AIC_c < 2$. RM = regularization multiplier (β), FC = feature classes, LQ = Linear, Quadratic.

Model	RM	FC	AIC_c	ΔAIC_c
1	4.0	LQ	7574.316	0.000
2	3.5	LQ	7574.389	0.070
3	4.5	LQ	7574.561	0.245
4	3.0	LQ	7574.785	0.470
5	5.0	LQ	7575.125	0.809
6	2.5	LQ	7575.509	1.193

Appendix 2 Supplementary Figures

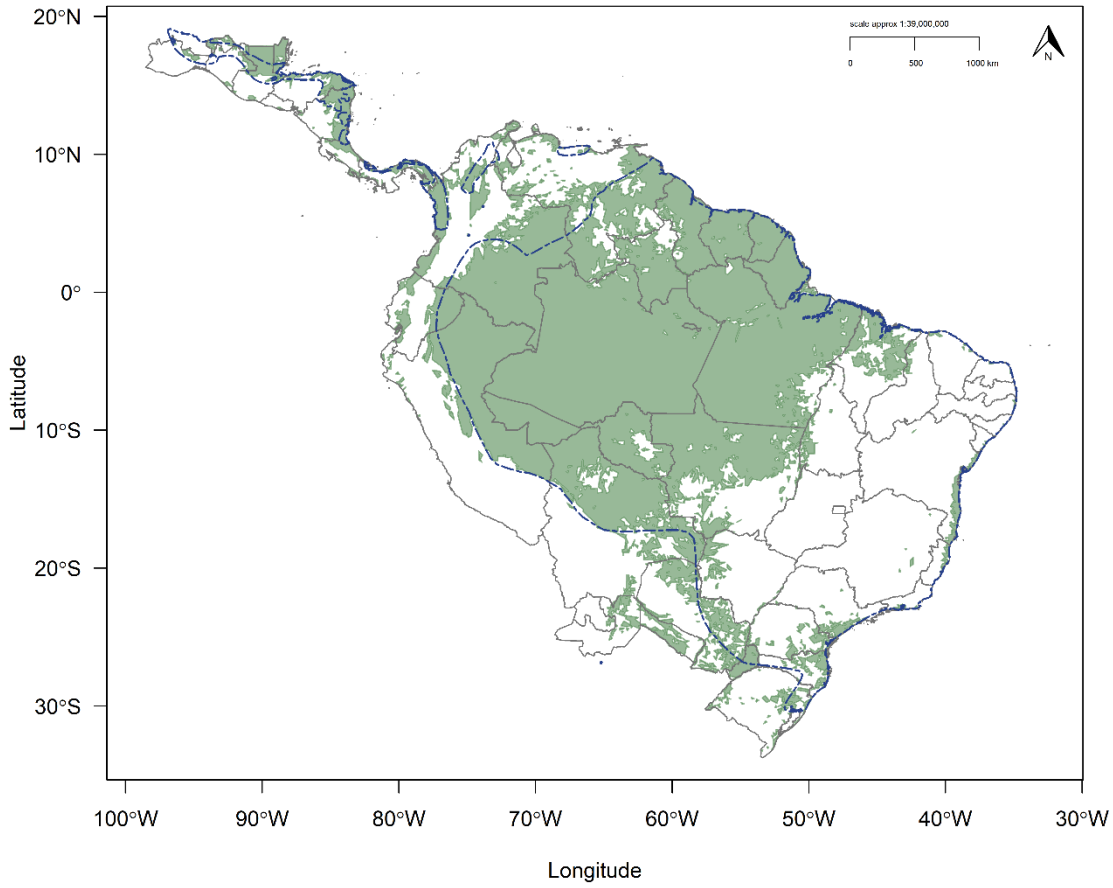


Figure S5.1. Reclassified binary Habitat Suitability Model (threshold = 0.345) for the harpy eagle. Pale green area is habitat above the 0.345 threshold, white areas below the threshold. Blue polygons define current IUCN range map for the harpy eagle as a comparison to the HSM prediction. Grey borders define national boundaries and internal state boundaries for Argentina, Brazil, and Mexico.

6. Reduced range size and protected area coverage for the harpy eagle predicted from multiple climate change scenarios.

6.1 Abstract

Climate change is expected to have a profound impact on range limits for many taxa, either forcing species to shift distribution tracking preferred climates, or contracting preferred climate space. Protected areas are an important tool to mitigate these negative effects but are static by design and thus do not account for future projections of species distributions. The harpy eagle (*Harpia harpyja*) is a large raptor with a broad range across lowland Neotropical forests. Due to its large range, harpy eagle distribution may not be adversely affected by climate change. However, when combined with habitat loss harpy eagle range size could contract. Here, I use spatial point process models fitted with climatic, topographic and landcover variables to identify current distribution, and project to 24 future climate scenarios, using three General Circulation Models (GCMs), and two emission scenarios between the years 2030-2090. The current model identified a core range across Amazonia and the Guiana Shield, with evergreen forest (71 %), mean diurnal temperature range (13 %), and elevation (6 %) the most important predictors. The reclassified current model estimated a range size of ~7.6 million km^2, with the IBA network covering 18 % of habitat (~1.4 million km^2) within this range. Range size was predicted to decrease on average by 7.3 % by 2090 under the lower emissions scenario, and 14.4 % under the higher emissions scenario. The IBA network would cover 3.3 % less distribution area under a lower emissions scenario by 2090 and 14 % less area under the higher emissions scenario. Under the 2090 higher emissions scenario, a core distribution area is predicted to remain across northern

Amazonia, the Guiana Shield and the Caribbean coast of Central America. Southern Amazonia is predicted to have the greatest reduction in range size and subsequently highest loss of harpy eagle habitat within the IBA network.

6.2 Introduction

Climate change is predicted to have a significant impact on the distribution of many bird species (Crick 2004; Pearce-Higgins & Green 2014), but with individual species likely to have differing responses to a changing climate (Pettorelli 2012). Therefore, assessing the threat level to each species is required, along with a species-specific assessment of adaptability to change. Even though the exact mechanisms limiting species distributions are often unclear (Journé *et al.* 2020), ultimately climatic conditions often determine where bird species are distributed (Huntley *et al.* 2007; Barnagaud *et al.* 2011; Pearce-Higgins & Green 2014). Increasing temperatures interacting with extreme climates, are predicted to have the greatest impact on bird populations at higher latitudes or elevations, driving poleward and upslope elevational range shifts (Şekercioğlu *et al.* 2008; Freeman *et al.* 2018). However, in lowland tropical regions, where precipitation is a key determinant of avian distributions (Şekercioğlu *et al.* 2012; Pearce-Higgins & Green 2014), climate change may not necessarily result in poleward range shifts but in multi-directional range shifts and contractions (Böhning-Gaese & Lemoine 2006; VanDerWal *et al.* 2013; de Moraes *et al.* 2020; Sutton *et al.* 2020).

Although temperature increases are predicted to be lower in the tropics compared to higher latitudes (IPCC 2014), populations of tropical bird species may be amongst the most vulnerable to climate change (Şekercioğlu *et al.*

2012). The expected negative effects of warming and drought on tropical species adapted to narrow thermal tolerances may lead to reductions in distribution and potential extinctions (Harris *et al.* 2011). In the Neotropics, projected rates of warming are expected to be highest in central South America (da Costa *et al.* 2010; Pearce-Higgins & Green 2014), with increasing drought conditions and reduced precipitation throughout the pan-Amazonian region, an area largely covered by climate-regulating tropical forests (Coe *et al.* 2017). Within the Neotropical avifauna, hawks and eagles (family: Accipitridae) may be particularly affected by climate change, because they generally exist at low population densities (Whitacre 2012) and are sensitive to habitat loss and fragmentation (Newton 1979; Krüger & Radford 2008). Factoring in the potential for range shifts and contractions adds another potential threat to this group in increasingly human-dominated landscapes.

The harpy eagle (*Harpia harpyja*) is a large Neotropical raptor with a broad but contracting range across Central and South America, with reductions in range size driven by habitat loss and fragmentation (Miranda *et al.* 2019; Sutton *et al.* 2021). The harpy eagle is classified as 'Near Threatened' on the International Union for the Conservation of Nature (IUCN) Red List (Birdlife International 2017) but is considered endangered or locally extinct in Central America and in the Atlantic Forest of Brazil (Vargas González *et al.* 2006). Harpy eagles are habitat specialists of lowland tropical forest (see Chapter 5), with habitat loss and persecution the current primary threats facing the species (Vargas González *et al.* 2006). Although the harpy eagle has a broad distribution, changing climatic conditions interacting with deforestation, could result in range contraction and potential shifts in the species distribution. As a habitat-specialist

raptor with low reproductive output, the harpy eagle may be particularly susceptible to the effects of climate change (Huntley *et al.* 2006), because it may struggle to adapt rapidly enough to changing conditions and resources (Krüger & Radford 2008; Miranda *et al.* In review).

Species that inhabit lowland areas without extensive topographical diversity may need to move long distances to track their preferred climate (Anciães & Peterson 2009; Harris *et al.* 2011; Şekercioğlu *et al.* 2012). For the harpy eagle, climate change could result in potential shifts or contraction in the species range, following its strong reliance on lowland tropical forest and the associated climate and resources (Miranda *et al.* 2019; Sutton *et al.* 2021). When coupled with anthropogenic factors such as deforestation, which is increasing in lowland tropical forests (Hansen *et al.* 2008), the habitat left for the harpy eagle may be considerably less in the future than is present now (see Chapter 5). Protected areas are an important tool for preserving the most critical areas to mitigate the various threats facing many species, such as habitat loss (Rodrigues & Cazalis 2020). However, in a changing climate identifying the areas where species ranges are predicted to shift or contract is a key priority for protected area designation to ensure continued coverage into the future (Blair *et al.* 2012; Şekercioğlu *et al.* 2012).

Globally, tropical moist forests have a relatively high percentage of protected area coverage, compared with other biomes (Wright 2005). Nevertheless, protected areas in tropical regions are predicted to be most vulnerable to climate change (Hoffman & Beierkuhnlein 2020). For birds, Important Bird and Biodiversity Areas (IBAs, BirdLife International 2019) are a key protected area

network, with extensive global coverage in areas of highest priority for endangered and endemic bird species (Donald *et al.* 2019). IBAs specifically target key areas that protect the long-term viability of bird populations, along with all the other biota associated with these key areas. Thus, as well as birds, IBAs also protect areas of high biodiversity and are used as a template for Key Biodiversity Areas (KBAs, IUCN 2016) an entire global protected area network (IUCN 2016; Donald *et al.* 2019). Therefore, how effective the IBA network will be for covering future harpy eagle distribution under climate change is a key question for setting spatial conservation planning priorities (Şekercioğlu *et al.* 2012).

Here, I use Species Distribution Models (SDMs) developed in a spatial point process regression framework to identify distributional constraints from harpy eagle occurrences fitted to a range of climatic, topographical, and landcover variables. I then use the current model and future climate projections to predict future distribution using a range of climate change scenarios. Specifically, I set out a baseline assessment of the range-wide impact of climate change on harpy eagle distribution using both lower and higher future emission scenarios between the years 2030-2090. Based on the future projections, I then identify areas where current IBA network coverage will continue or be lost. I aim to apply spatial statistical modelling to inform range-wide conservation planning to: **(1)** estimate the current distributional range for the harpy eagle, **(2)** predict future distribution based on multiple climate change scenarios, and **(3)** quantify how effective the current IBA network is for covering areas of future harpy eagle distribution.

6.3 Methods

6.3.1 Occurrences

Harpy eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, The Peregrine Fund 2018) a data information system for all raptor species. For the harpy eagle, GRIN consists of occurrence data from the Global Biodiversity Information Facility (GBIF 2019a), which are mostly eBird records (79 %, Sullivan *et al.* 2009), along with two additional datasets of observations (Vargas González & Vargas 2011; Miranda *et al.* 2019). Occurrences were cleaned by removing duplicate records, and those with no geo-referenced location. Only occurrences recorded from 1970 onwards were included to temporally match the timeframe of the climatic predictors. A 5 km spatial filter was applied between each occurrence point using the 'geoThin' function in the R package enmSdm (Smith 2019). Using a 5 km filter approximately matches the resolution of the raster data (~4.5 km) and reduces the effect of biased sampling (Kramer-Schadt *et al.* 2013). A total of 1146 geo-referenced records were compiled after data cleaning. Applying the 5 km spatial filter resulted in a filtered subset of 692 harpy eagle occurrence records for use in the models.

6.3.2 Environmental predictors

Predictors were selected *a prioiri* based on harpy eagle biology (Vargas González & Vargas 2011; Miranda *et al.* 2019; Sutton *et al.* 2021). A total of nine continuous predictors (Table 6.1) were included at a spatial resolution of 2.5 arc-minutes (~4.5km resolution), a suitable resolution for capturing environmental variation across climatically-stable lowland regions with low terrain complexity (Fick & Hjimans 2017). Raster layers were cropped using a delimited polygon consisting of all known range countries (including Formosa,

Jujuy, Misiones and Salta provinces in northern Argentina, and Chiapas, Oaxaca and Tabasco states in southern Mexico), to extend into potential future areas of marginal habitat on the distribution edges. This provides more realistic model predictions by focusing on the accessible area available to the harpy eagle (Barve *et al* 2011). Further, reducing the background area used for testing points used in model evaluation also limits model overfitting (Radosavljevic & Anderson 2014). All variables showed low collinearity and thus all nine were included as predictors in model calibration (Variance Inflation Factor (VIF) < 6).

Table 6.1. Environmental variables used as predictors in current and future Species Distribution Models for the harpy eagle.

Predictor	Source	Citation
Mean diurnal temperature range (°C)	WorldClim v2.1	Fick & Hjimans 2017
Isothermality (%)	WorldClim v2.1	Fick & Hjimans 2017
Temperature seasonality (SD, °C)	WorldClim v2.1	Fick & Hjimans 2017
Precipitation wettest month (mm)	WorldClim v2.1	Fick & Hjimans 2017
Precipitation warmest quarter (mm)	WorldClim v2.1	Fick & Hjimans 2017
Terrain Ruggedness Index (TRI)	ENVIREM	Title & Bemmels 2018
Elevation (m)	EarthEnv	Amatulli *et al.* 2018
Evergreen forest (%)	EarthEnv	Tuanmu & Jetz 2014
Cultivated (%)	EarthEnv	Tuanmu & Jetz 2014

Five climatic predictor variables were downloaded from the WorldClim v2.1 database (Fick & Hjimans 2017). WorldClim variables are interpolated from average monthly weather station climate data (9000-60,000 stations) from 1970-2000. WorldClim v2.1 improves on the previous WorldClim v1.4 by incorporating remote-sensed satellite data for areas with low weather station density. Two topographical predictors were sourced from the ENVIREM (Title & Bemmels 2018) and EarthEnv (www.earthenv.org) databases, used to provide

measures of topographical heterogeneity, where species may find refugia from future climatic conditions (Austin & Van Niel 2010; Meineri & Hylander 2017). Elevation and Terrain Roughness Index (TRI) are both key topographic variables influencing harpy eagle distribution (Vargas González & Vargas 2011; Vargas González *et al.* 2020; Sutton *et al.* 2021) and including topography in climate change SDMs can improve model predictions (Luoto & Heikkinen 2008; Virkkala *et al.* 2010). Elevation was derived from a digital elevation model product from the 250 m Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010, Danielson & Gesch 2011). TRI was derived from the 30 arc-sec resolution Shuttle Radar Topographic Mission (SRTM30, Becker *et al.* 2009).

The two measures of percentage landcover (Evergreen forest and Cultivated) are consensus products derived from satellite remote-sensing, integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) at 30 arc-sec (~1km) spatial resolution. Both landcover layers were resampled to a spatial resolution of 2.5 arc-minutes using bilinear interpolation. Full details on methodology and image processing can be found in Tuanmu & Jetz (2014). Landcover predictors were included following IUCN guidelines for modelling climate change distributions (IUCN 2019), with both evergreen forest and cultivated land key predictors for harpy eagle distribution (see Chapter 5). Including landcover in SDMs improves future climate change predictions (Pearson *et al.* 2004; Stanton *et al.* 2012), accounting for the dynamic nature between climate and land use, and despite the limitations of using current land use in future predictions (Beale *et al.* 2008; Renwick *et al.* 2012; Stanton *et al.* 2012; Platts *et al.* 2019).

6.3.3 Species Distribution Models

SDMs were fitted using a point process modelling (PPM) framework employing the maximum entropy software, MAXENT (v3.4.1, Phillips *et al.* 2017). Internal model parameters were set to fit a PPM model treating occurrences as point intensity rather than grid cells, following the methodology set out by Renner *et al.* (2015). Recent theoretical work has demonstrated the equivalence of MAXENT to an inhomogeneous Poisson process (IPP; Fithian & Hastie 2013; Renner & Warton 2013; Renner *et al.* 2015), which is the most appropriate method for fitting presence-only data SDMs (Warton & Shepherd 2010). Within the MAXENT software, the complementary log-log (cloglog) transform was selected as a continuous index of environmental suitability, with 0 = low suitability and 1 = high suitability. Phillips *et al.* (2017) demonstrated the cloglog transform is equivalent to an IPP and can be interpreted as a measure of relative occurrence probability proportional to a species relative abundance.

A random sample of 10,000 background points were used as pseudo-absences (Barbet-Massin *et al.* 2012) and to sufficiently sample the background calibration environment (Guevara *et al.* 2018). Convergent threshold was set at 10^{-5} and iterations increased to 5000 from the default (500) allowing for model convergence. Optimal-model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich &Tsai 1989), to determine the most parsimonious model from two key MAXENT parameters: regularization multiplier and feature classes (Warren & Seifert 2011). Tuning MAXENT parameters results in more biologically relevant response curves, limits sampling bias, and reduces over-fitting in presence-only predictions (Merow *et al.* 2013; Radosavljevic & Anderson 2014). Only using

Linear and Quadratic feature classes results in less complex and more realistic predictions (Merow *et al.* 2013; Guevara *et al.* 2018). Omitting Threshold and Product feature classes generally increases model performance and gives more biologically meaningful model interpretations (Phillips *et al.* 2017). Hinge features were used initially but resulted in unrealistic response curves, so were omitted from model calibration (Guevara *et al.* 2018).

For the current distribution, eighteen candidate models of varying complexity were built by comparing a range of regularization multipliers from 1 to 5.0 in 0.5 increments, and two feature classes (Linear and Quadratic) in all possible combinations using the 'block' method of cross-validation (k = 5) in the ENMeval package in R (Muscarella *et al.* 2014). Block partitioning masks the geographical structure of the data according to latitude and longitude lines, dividing all occurrences into four spatially independent bins of equal numbers. Masking the geographical structure of test-data means the models are projected onto an evaluation region not included in the calibration process. All occurrence and background test points are assigned to their respective bins dependent on location, further reducing spatial autocorrelation between testing and training localities (Muscarella et al. 2014, Radosavljevic and Anderson 2014). The block method was chosen because it reduces the possibility of encountering non-analogue climate conditions when transferring model predictions in time (Radosavljevic and Anderson 2014).

For future predictions, 24 SDMs were built using three earth system General Circulation Models (GCMs, Table 6.2) from the Coupled Model Intercomparison Project Phase 6 (CMIP6; Eyring *et al.* 2016). Two future emission scenarios

were used across four time periods: 2030 (averaged over 2021-2040), 2050 (averaged over 2041-2060), 2070 (averaged over 2061-2080) and 2090 (averaged over 2081-2100). A range of projections were used to assess the magnitude of climate change from the short to long term. Three GCMs were used to account for variation in model output sensitivity, and any uncertainty in single model predictions (Pearce-Higgins & Green 2014; Lutz *et al.* 2016). Data were downloaded from the WorldClim database (v2.1, Fick & Hjimans 2017) for two CMIP6 emission scenarios or Shared Socioeconomic Pathways (SSPs): SSP245 and SSP585. SSP245 represents limiting warming to < 3°C by 2100, and SSP585 corresponds to a 'worst-case scenario' where no climate policy actions are implemented with CO_2 emissions reaching > 120 gigatonnes annually by 2100 (Riahi *et al.* 2017). Finer resolutions (e.g. 30 arc-seconds) of future climatic data are currently unavailable for CMIP6 projections in WorldClim v2.1, thus 2.5 arc-minutes was used as a suitable resolution for the broad scale analysed here. All internal MAXENT parameters used for the current distribution model were kept for the future distribution models and predicted using the 'projection layers' function in the MAXENT software.

Table 6.2. General Circulation Models (GCMs) from the Coupled Model Inter-comparison Project Phase 6 (CMIP6) used to predict future harpy eagle distribution.

General Circulation Model (GCM)	Acronym	Citation
Canadian Earth System Model v5	CanESM5	Swart *et al.* 2019
CNRM Earth System Model v2.1	CNRM-ESM2-1	Séférian *et al.* 2020
Model for Interdisciplinary Research on Climate - Earth System v2 for Long-term simulations	MIROC-ES2L	Hajima *et al.* 2020

6.3.4 Model evaluation

Optimal model selection was evaluated using both threshold-independent and threshold-dependent measures (Radosavljevic & Anderson 2014). Area Under the Curve (AUC) is a non-parametric, threshold-independent measure representing an overall value of model performance across all thresholds, with AUC = 1.0 being the maximum predictive performance, and an AUC = 0.5 being no better than a random prediction (Franklin 2009). AUC_{DIFF}, the difference in AUC values from the training and test models (AUC_{TRAIN} - AUC_{TEST}) was used to quantify model over-fitting (Muscarella *et al.* 2014), with a value close to zero indicating a low over-fit model (Warren & Seifert 2011). AUC has been criticized as a measure of model performance for presence-background SDMs (Lobo *et al.* 2008; Jiménez-Valverde 2012). Thus, AUC metrics were used here as a measure of optimal model selection, best suited to comparing a range of candidate models and not as a test of final model predictive performance.

Omission rates report the proportion of training points that are outside of the model when converted into a threshold binary prediction, evaluating discriminatory ability at a specified threshold. Lower omission rates show improved discrimination between suitable and unsuitable pixels (indicating higher performance), whilst overfitted models show higher omission rates than expected by theory (Radosavljevic & Anderson 2014). A single threshold-dependent measure was calculated based on the 10% training presence omission rate (OR10) threshold. For low over-fit models the expectation for OR10 is a value of 0.10 (Muscarella *et al.* 2014). Response curves, percent contribution and permutation importance were used as estimates for variable performance within the optimal calibration model. Percent contribution is the

proportion of each variable to model training gain dependent on the algorithm, whereas permutation importance is independent of the algorithm path and represents the importance of a given value on the AUC training values (Phillips *et al.* 2006). Pair-wise niche overlap metrics were calculated for all future continuous distributions to quantify how predictions from the three GCMs differed in geographic space using Schoener's *D* (Schoener 1968, Warren *et al.* 2008), which ranges from 0 (no overlap) to 1 (identical predictions).

Final model predictions were tested against random expectations using partial Receiver Operating Characteristic ratios (pROC), which estimate model performance by giving precedence to omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios range from 0 – 2 with 1 indicating a random model. Function parameters were set with a 10% omission error rate, and 1000 bootstrap replicates on 50% test data to determine significant ($\alpha = 0.05$) pROC values >1.0 in the R package ENMGadgets (Barve & Barve, 2013). Continuous Boyce index (CBI) was used as a threshold-independent evaluation metric (Hirzel *et al.* 2006), measuring how much environmental suitability predictions differ from a random distribution of observed presences (Boyce et al. 2002). It is consistent with a Spearman correlation (r_s) with values of CBI ranging from -1 to +1, with positive values indicating predictions consistent with observed presences, values close to zero no different than a random model, and negative values indicating areas with frequent presences having low environmental suitability. CBI evaluation was calculated on 20% test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019).

6.3.5. Reclassified models

To calculate current and future distribution area, all continuous models were reclassified as binary threshold predictions. From the three GCM future predictions for each year, mean predictions were calculated from the continuous outputs for each future emissions scenario. All pixels equal to or greater than the median value of 0.396 from the continuous model were used as a suitable threshold for conservation planning (Liu *et al.* 2005; Rodríguez-Soto *et al.* 2011; Portugal *et al.* 2019). The IBA network polygons (as of September 2019; BirdLife International 2019) were then clipped to the reclassified area, establishing those IBAs covering pixels of habitat suitability ≥ 0.396 threshold. The IBA shapefile was cropped to the harpy eagle range extent, and then intersected with each mean binary prediction to calculate IBA coverage (km^2). Geospatial analysis and modelling were performed in R (v3.5.1; R Core Team, 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017), rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundle 2019) and sp (Bivand *et al.* 2013) packages.

6.4 Results

6.4.1 Current Distribution Model

The best-fit model ($\Delta AIC_c = 0.0$) used feature class parameters Linear and Quadratic, with a regularization multiplier of $\beta = 1$. Optimal model selection metrics using 'block' cross-validation had moderate to high predictive performance ($AUC_{TRAIN} = 0.780$; $AUC_{TEST} = 0.755$). Model overfitting was low ($AUC_{DIFF} = 0.025$), with discrimination ability close to the expected omission rate threshold (OR10 = 0.15). The final predictive model was robust against random expectations (pROC = 1.482 ±0.052, range=1.321-1.629), with high calibration accuracy between predicted environmental suitability and test occurrence points (CBI = 0.928). The current distribution model defined a large continuous range across Amazonia and the Guiana Shield, with a corridor running north from the Chocó region of Colombia through Central America along the Caribbean coast (Fig. 6.1). Distribution across the largely deforested Atlantic Forest region in Brazil was patchy and fragmented, mainly confined to the far south-east of the region. The reclassified threshold prediction (median = 0.396) estimated a range size of climatically suitable habitat totalling 7,617,932 km^2. Within this distributional area the current IBA network covered 18.2 % (1,388,412 km^2) of habitat for the harpy eagle (Fig. 6.2).

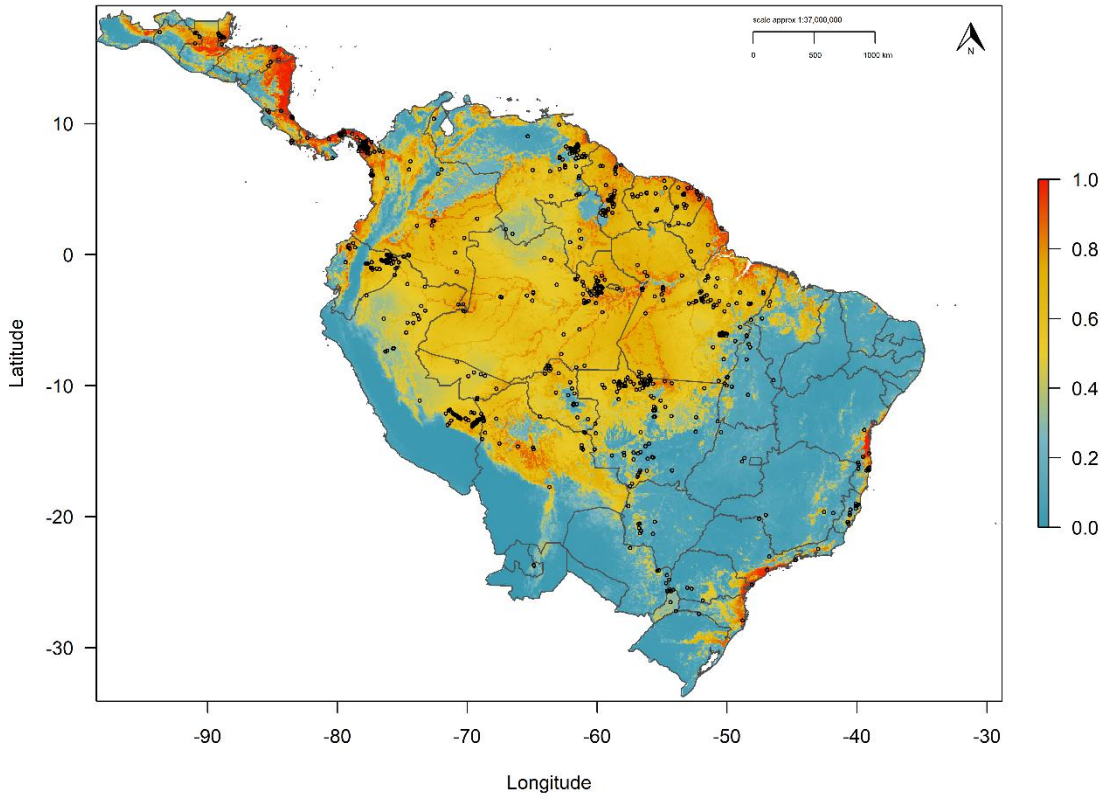


Figure 6.1. Predicted continuous distribution model for the harpy eagle. Map denotes cloglog prediction with values closer to 1 having higher environmental suitability for harpy eagle occurrence. Black points define known harpy eagle occurrences.

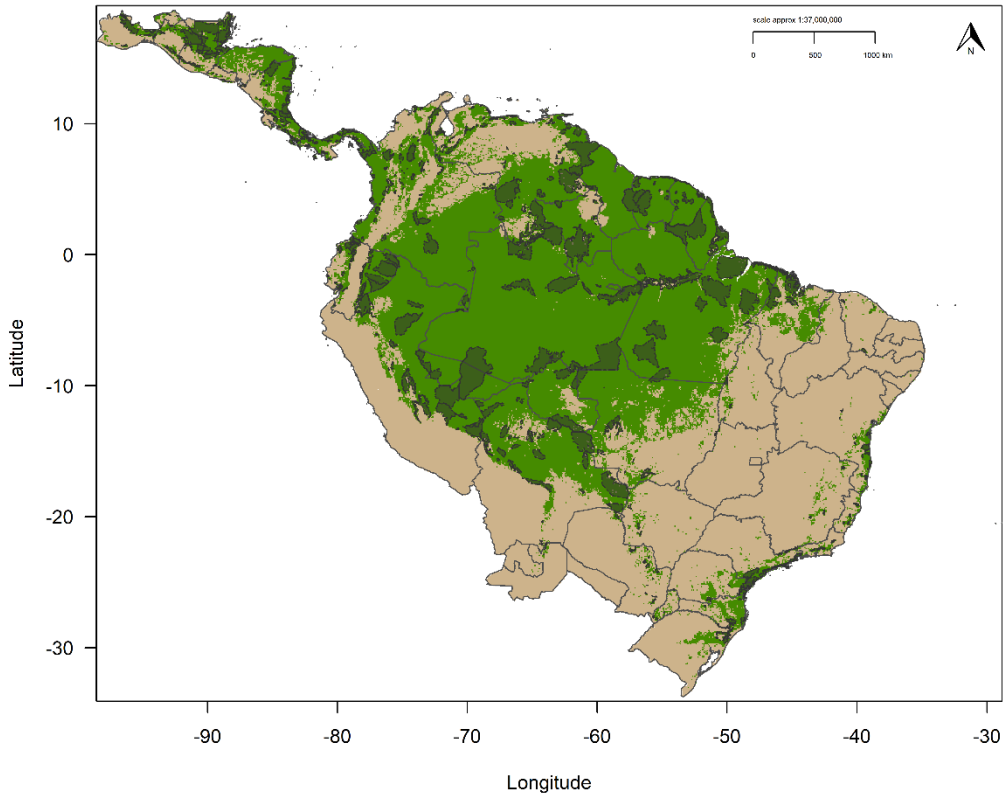


Figure 6.2. Reclassified prediction using the median threshold (0.396). Green areas are predicted harpy eagle habitat, beige areas predicted unsuitable habitat. Black bordered polygons define the current Important Bird and Biodiversity Area (IBA) network within the median threshold prediction.

6.4.2 Variable Importance

Four variables contributed 92.9 % to model prediction (Table S6.1), with evergreen forest the highest contributor (71.2 %), followed by mean diurnal temperature range (12.9 %), elevation (5.6 %), and isothermality (3.2 %). Evergreen forest had peak suitability at 60-70 % proportion forest cover, with peak suitability for zero or low proportion of cultivated land (Fig. 6.3). Mean diurnal temperature range had a suitability range of 5 °C, as expected in the relatively stable climatic conditions of lowland tropical forests. Topographic

areas had highest suitability between 0-500 m elevation and low terrain roughness with TRI peak suitability ~100. Isothermality peaked at 40-50 %, reflecting the constant annual temperatures harpy eagles need in lowland tropical forests. Precipitation in the wettest month peaked at 500-600 mm/month, with highest suitability for precipitation in the warmest quarter between 700-800 mm.

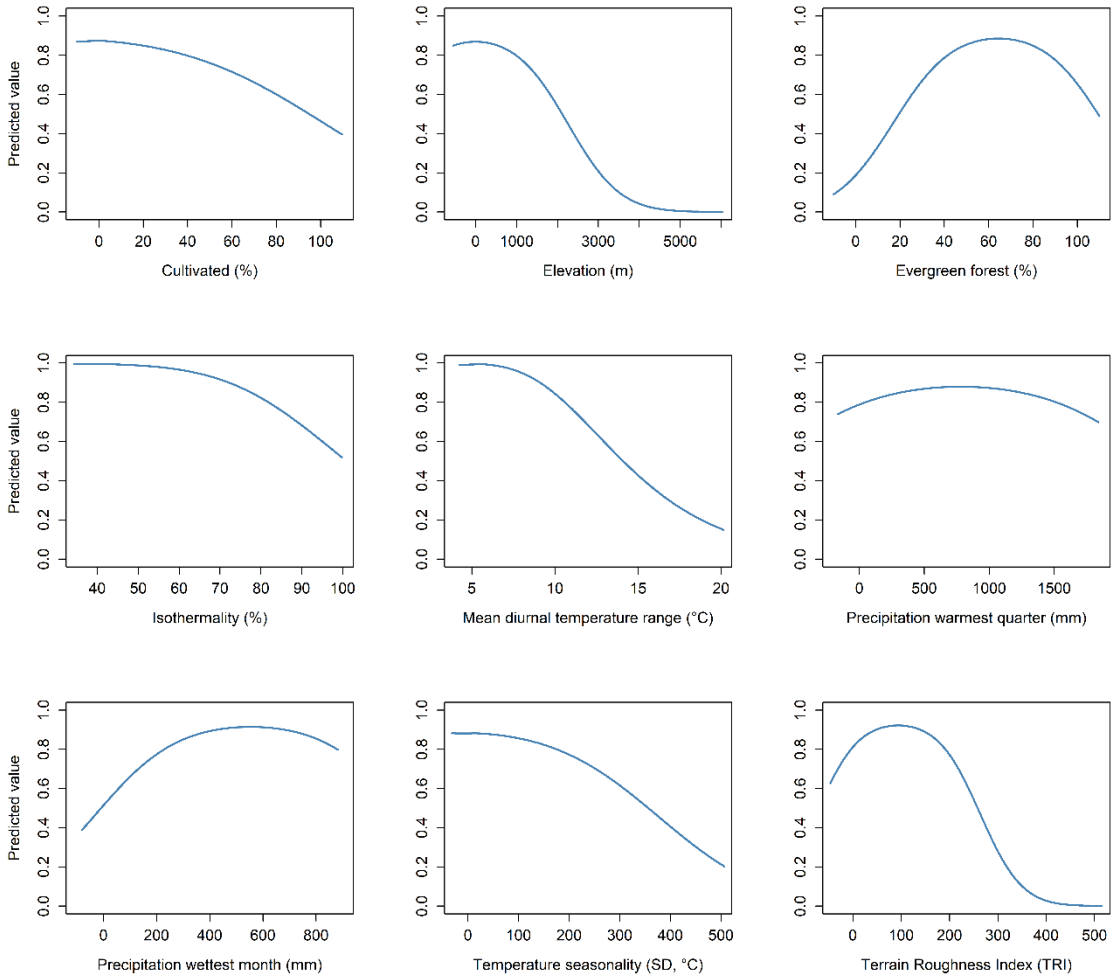


Figure 6.3. Response curves for each environmental variable used as predictors in the current distribution model for the harpy eagle.

6.4.3 Future distribution models

The mean binary GCM predictions showed a steady decline in range size in both emission scenarios (Table 6.3). Under the lower emissions scenario (SSP245), mean range size is predicted to decrease by 2 to 7 % from 2030 to 2090 (Table 6.3; Fig. S6.1). Under the higher emissions scenario (SSP585), mean range size is predicted to decrease by 5 to 14 % from 2030 to 2090 (Table 6.3; Fig. S6.2). From all individual future predictions there was high correlation between GCMs in where future geographic space will persist (Table S6.2; Figs. S6.3-S6.10), but with some variation in the amount of area predicted to contract (Tables S6.3-S6.4).

Table 6.3. Predicted percent change in future range size (km^2) for the harpy eagle for the years 2030, 2050, 2070 and 2090 using lower (SSP245) and higher (SSP585) emissions climate change scenarios from three General Circulation Models (GCMs). All values are %.

	2030		2050		2070		2090	
GCM / SSP	245	585	245	585	245	585	245	585
CanESM5	-3.9	-12.7	-9.7	-15.7	-13.5	-19.4	-20.8	-28.6
CRNM-ESM2-1	-0.9	-0.3	0.2	-0.3	0.2	-0.7	1.6	-4.7
MIROC-ES2L	-0.7	-3.2	-5.1	-2.5	-5.5	-6.1	-2.3	-10.1
Mean	-1.8	-5.4	-4.9	-6.1	-6.3	-8.7	-7.3	-14.4

Using the CanESM5 climate projection as the most sensitive GCM, all future climate scenarios predicted a consistent contraction in range size across southern and central Amazonia (Figs. 6.4-6.5). A core distribution area is predicted to persist across the wider pan-Amazonian region and Guiana Shield under both emission scenarios from 2030-2050. However, from 2070 to 2090 under the higher emissions scenario (Fig. 6.5), the distribution area is restricted

to northern Amazonia, the Guiana Shield, and the Caribbean coast of Central America. Southern and south-western Amazonia is predicted to have the greatest reductions in distribution area, but with an area adjacent to the east Andean slope in Bolivia and Peru persisting to 2090 under the higher emissions scenario.

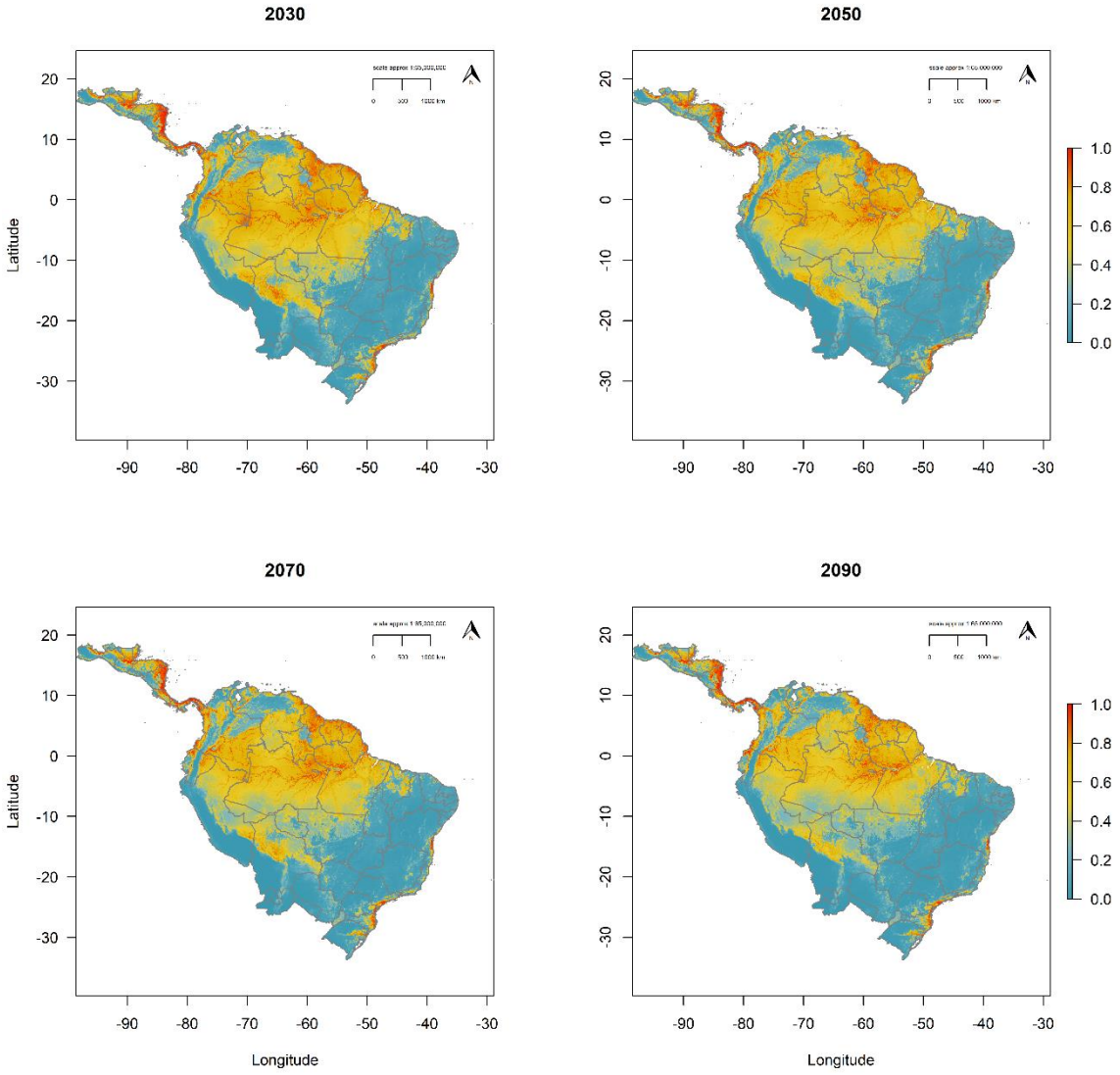


Figure 6.4. Continuous predictions from the CanESM5 general circulation model for harpy eagle distribution using the SSP245 emissions scenario across four future climate change timeframes.

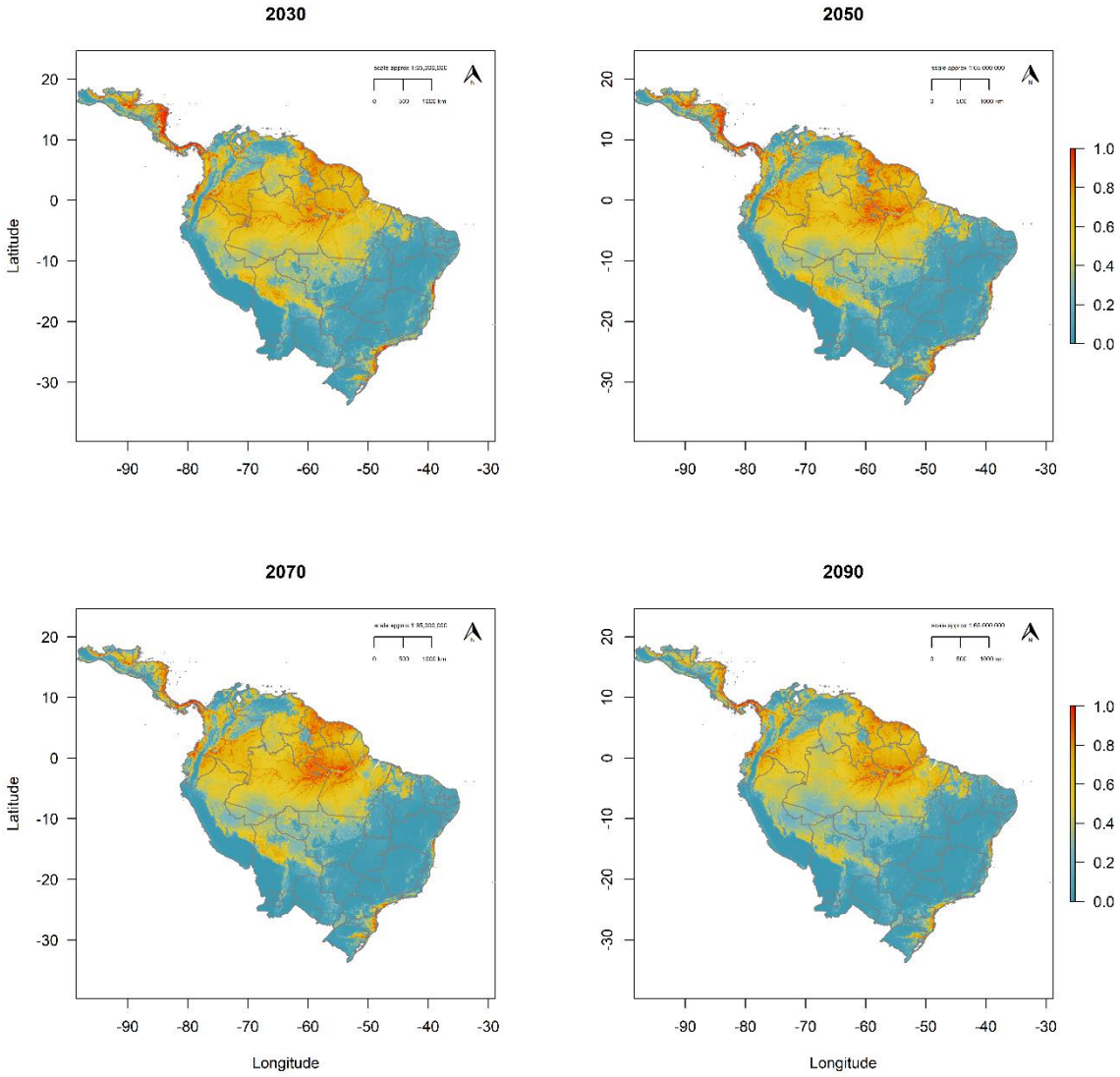


Figure 6.5. Continuous predictions from the CanESM5 general circulation model for harpy eagle distribution using the SSP585 emissions scenario across four future climate change timeframes.

6.4.4 IBA network coverage

Using the mean GCM projections under the lower emissions scenario (SSP245), the current IBA network would provide similar coverage from 2030 to 2050 with percentage losses between 0.2 and 1.3 % (Table 6.4). By 2070, there would be 4.1 % less distribution area covered, but 3.3 % less distribution area by 2090 (Table 6.4). Under the higher emissions scenario, decreases in IBA network coverage of 2.7 and 2.2 % are predicted for 2030 and 2050 respectively, with 6 % less coverage by 2070 and 14 % less IBA coverage by 2090 (Table 6.4).

Table 6.4. Mean area and percent loss or gain of future harpy eagle distribution within the current IBA network from eight climate change scenarios from 2030-2090.

SSP245	Year	Area (km^2)	% gain/loss
	2030	1,385,341	-0.2
	2050	1,370,469	-1.3
	2070	1,331,280	-4.1
	2090	1,342,220	-3.3
SSP585			
	2030	1,351,043	-2.7
	2050	1,357,640	-2.2
	2070	1,304,577	-6.0
	2090	1,194,030	-14.0

To identify a ‘worst-case scenario’ for 2090 the CanESM5 climate projection was used as the most sensitive GCM under the SSP585 higher emissions scenario. This climate change outcome would result in an ~29 % reduction in range size to 5,441,364 km^2 (Table 6.3; Table S6.4; Fig. 6.6), with the current IBA network coverage reduced by ~32 % to 946,779 km^2 (Fig. 6.6). Most

protected area losses are predicted within south-west Brazil across the states of Acre, Rondônia, Mato Grosso and southern Amazonas, and the bordering regions in eastern Bolivia and Peru. However, a broad area adjacent to the east Andean slope in Bolivia and Peru would still retain IBA coverage.

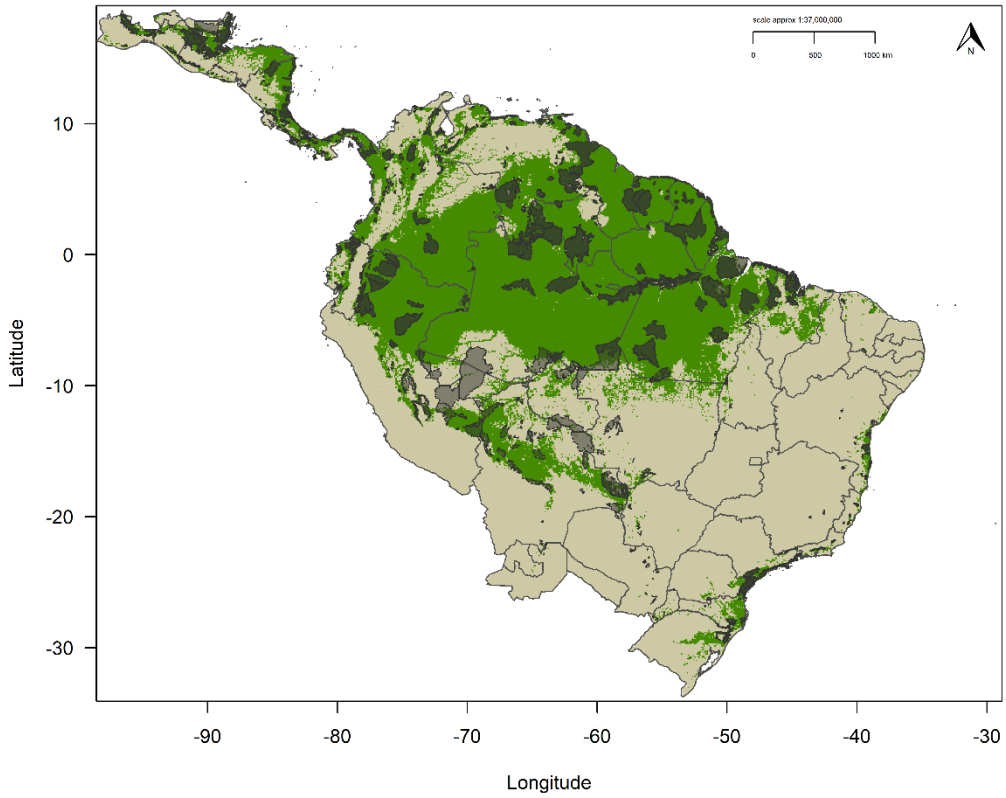


Figure 6.6. Reclassified 'worst-case scenario' prediction for 2090 under the higher emissions scenario (SSP585) using the CanESM5 Global Circulation Model (GCM) projection. Black bordered polygons show continued coverage of the current Important Bird and Biodiversity Area (IBA) network and grey polygons where future harpy eagle distribution will be lost within the IBA network.

6.5 Discussion

The results demonstrate how climate change could lead to range size contraction for the harpy eagle and subsequently reduce coverage within the current IBA network, mainly across the southern extent of the species range. Evergreen forest was the most important predictor, followed by mean diurnal temperature range and elevation, predicting a core range across Amazonia and the Guiana Shield. The reclassified model estimated a current distribution area totalling ~7.6 million km^2, with the current IBA network covering 18 % (~1.4 million km^2) of this distributional area. By 2090, mean range size was predicted to decrease by 7 % under the lower emissions scenario, and 14 % under the higher emissions scenario. By 2090 under the higher emissions scenario, a core distribution area is predicted to remain across northern Amazonia, the Guiana Shield and the Caribbean coast of Central America. By 2090, there would be 3 % less mean distribution area covered by the IBA network under a lower emissions scenario and 14 % less IBA coverage under the higher emissions scenario. Southern Amazonia is predicted to have the greatest reductions in distribution area and subsequently highest loss of habitat within the IBA network.

6.5.1 Current distribution

Estimating current and future species distributions using SDMs was established mainly using climatic variables (Pearson & Dawson 2003; Thuiller 2004; Hijmans & Graham 2006; Huntley *et al.* 2006), especially at continental extents where climate is expected to exert a stronger influence on distribution (Pearson & Dawson 2003, Huntley *et al.* 2007). However, species range limits are dependent on the interaction of multiple factors other than climate such as land

cover (Renwick *et al.* 2012; Stanton *et al.* 2012) and topography (Luoto & Heikkinen 2008; Virkkala *et al.* 2010; Hof *et al.* 2012). The models here demonstrate that including land cover results in a more realistic range estimate for the harpy eagle compared to using solely climatic and topographical predictors (Sutton *et al.* 2021). Evergreen forest was more important for predicting harpy eagle distribution than any climate variable, with a narrow mean diurnal temperature range the most important climatically. Because the harpy eagle is a habitat specialist of lowland tropical forests (see Chapter 5), it follows that high proportion of evergreen forest, lower elevation, and stable temperatures would have the greatest influence on determining the species geographic range. Thus, the interaction between vegetation, climate, and topography best explains harpy eagle range limits, rather than relying solely on climate and topography (Sutton *et al.* 2021).

In lowland tropical regions daily and seasonal temperatures are relatively constant (Nieuwolt 1977), thus it follows that a mean diurnal temperature range of 5 °C should contribute the highest percent to model prediction. This narrow temperature range tolerance is common amongst many tropical bird species (Şekercioğlu *et al.* 2008), and ultimately may be a key factor in how a changing climate may affect the distribution of many tropical species that have evolved within narrow thermal limits (Harris *et al.* 2011; Şekercioğlu *et al.* 2012). Aside from temperature, precipitation may be as important for determining tropical bird species ranges (Şekercioğlu *et al.* 2012; Pearce-Higgins & Green 2014). For the harpy eagle, both monthly and seasonal rainfall only contributed small percentages to model prediction (see Fig. 6.3). This suggests that precipitation may not be a direct determinant limiting harpy eagle distribution, but that moist

tropical forest driven ultimately by high rainfall is a more useful proximate predictor. Indeed, > 70 % forest cover may be required to maintain the forest-dependent rainfall regime in Amazonia (Silva Dias *et al.* 2002; Soares-Filho *et al.* 2006), which correlates with the peak suitability for evergreen forest identified for harpy eagles here.

6.5.2 Future distributions

Unlike the general poleward shifts in distribution predicted for many temperate bird species, the core distribution for the harpy eagle will remain in equatorial regions of its range and is not predicted to shift. By 2090 the main distribution strongholds will remain across northern Amazonia, the Guiana Shield, and parts of Central America assuming that land cover remains static, which seems unlikely. Including land use has gained wide support when predicting future distributions, even when land cover is a static variable derived from current land use layers (e.g. Pearson *et al.* 2004; Renwick *et al.* 2012; Stanton *et al.* 2012; Platts *et al.* 2019). Thus, including current land cover restricts the future models to those future areas predicted suitable both climatically and from land use, despite its unrealistic static nature for future predictions. Incorporating future land use scenarios (e.g. Hurtt *et al.* 2016) within the modelling framework would improve model predictions using a more dynamic approach (Beale *et al.* 2008; Huntley *et al.* 2010). Accounting for the rapid change in human-mediated land use (Powers & Jetz 2019), in particular across the Neotropics (Borges & Loyola 2020), would improve future forecasting efforts when combined with future climate change projections.

Projected paleoclimate SDMs for the harpy eagle have shown how the species range may have increased in size from the last glacial maximum (LGM) to the Mid-Holocene (Sutton *et al.* 2021). Indeed, during the LGM, harpy eagle spatial distribution was similar to that predicted for 2090 under the mean higher emissions scenario. However, the key difference now is that the rate and magnitude of climate change is occurring over decades (Parmesan & Yohe 2003), at a more rapid rate than that experienced from the LGM (~20,000 mya) to the Mid-Holocene (~ 6,000 mya). Under the lower emissions scenario (SSP245) projected mean distribution area losses are relatively small, even by 2090 (7.3%, Table 6.3), with consequently only small percentage losses within the IBA network by 2090 (3.3 %). Therefore, if the global community does act to reduce carbon emissions and keep global average temperatures below 3°C, then the outlook may not be as pessimistic, at least in terms of the future prospects for the harpy eagle. Further, if the harpy eagle is viewed as a surrogate species for the future extent of lowland tropical forest, then future climate change projections may be offset if climate change policy is enacted. However, this is underpinned on maintaining sufficient habitat, along with preferred climate space for lowland tropical forest biota (Guo *et al.* 2018; Senior *et al.* 2019).

6.5.3 Protected areas

Protecting large areas of key habitat is an important tool for species conservation (Rodrigues & Cazalis 2020) and should be prioritised in an ongoing effort to identify gaps in coverage, establishing an effective interconnected network (See Chapter 5; Rodrigues *et al.* 2004a; Rodrigues *et al.* 2004b). Whilst the current IBA network exceeds the protected area target

representation for harpy eagle habitat (10 %, see Chapter 5), future coverage under climate change may see this target reduced in the south of the species range. Brazil is predicted to lose most distribution area for the harpy eagle within the IBA network, mainly across the states of Acre, Rondônia, and Mato Grosso. Unfortunately, this area is one of the main agricultural frontiers in Brazil, where the 'arc of deforestation' is advancing rapidly (Coe *et al.* 2017; Miranda *et al.* 2020). Even though the models predict a reduced distribution area in the region, this may not necessarily mean that the harpy eagle will disappear from the area. As the modelling demonstrates, vegetation and climate are tightly linked in tropical forests (Coe *et al.* 2017), and if sufficient forest is maintained the harpy eagle may still persist at higher temperatures, as demonstrated for tropical forest birds in lowland New Guinea (Freeman & Beehler 2018). Thus, expanding protected areas and connecting habitat now across these states would be more effective and less costly in the long-term even if future climate is deemed less favourable (Hannah *et al.* 2007).

Whilst the core range of the harpy eagle across northern Amazonia and the Guiana Shield will still retain some level of coverage within the IBA network, this is based on current land cover remaining static until 2090. Because this future land use scenario is unlikely (Powers & Jetz 2019), expanding IBAs across northern Amazonia, the Guiana Shield, and further north into Central America, will be required to maintain a sufficient level of IBA coverage for the harpy eagle. Indeed, priority gaps in the IBA network have all been identified for the harpy eagle in north-west Amazonia, Guyana, and the Chocó- Darién ecoregion in Colombia (see Chapter 5). Establishing new IBAs in all these areas seems even more necessary now given the core area of future distribution projected to

remain in these regions. Even if the climate change models here are not entirely correct, maximising protected habitat now in the short-term would not be a wasteful use of resources. Spatial conservation planning would still be focused on current threats but would incorporate a climate change 'no regrets' principle (Hannah *et al.* 2007; Pearce-Higgins & Green 2014) based on best-practice modelling for potential future distribution.

Though the models here had high predictive power, I recognise limitations to this approach. The interpretation of the future distribution models should be taken as a maximum range extent, knowing that forest cover is predicted to decrease and cultivated land increase over the time period analysed here (Powers & Jetz 2019). Indeed, shifting seasonality in the tropics combined with rapid land use change is predicted to have a strongly negative impact on the range limits for many tropical taxa (Sodhi *et al.* 2012). Taking a process-based approach by sustaining the underlying mechanisms for adaptation is critical (Tobias *et al.* 2013). Maintaining habitat heterogeneity and connectivity between key areas of protected habitat linked to area-based conservation can prevent species extinction (Tobias *et al.* 2013). Thus, to be effective, protected areas need extensive habitat heterogeneity, topographical diversity, and cover wide elevational ranges (Sodhi *et al.* 2012). Therefore, including all these elements within the modelling process, as demonstrated here, is crucial to identify those areas predicted to remain most suitable into the future.

6.5.4 Conclusion

Changing climates have shaped species distributions over the aeons, yet the current magnitude and rate of human-mediated climate change, combined with

habitat loss, may result in significant contractions and shifts in species range limits (Parmesan & Yohe 2003; Travis 2003; Sodhi *et al.* 2011). Mainly due to its large range, the harpy eagle may not be the species most seriously affected by climate change compared to other tropical taxa (Gaston & Fuller 2009; Sodhi *et al.* 2011). Nevertheless, when combined with habitat loss, a changing climate may result in substantial losses in distribution for this raptor across the southern edge of its range. Thus, maintaining and expanding a network of large-sized IBAs that contain high habitat and climatic heterogeneity may be a solution within a fixed reserve network that is robust to future climate change (Carroll *et al.* 2010; Pearce-Higgins & Green 2014). This would not only benefit the harpy eagle, but as a large apex predator requiring large tracts of continuous tropical forest, it would benefit all the associated tropical forest biota within those protected areas.

6.7 Appendices

Appendix 1 Supplementary Tables

Table S6.1. Percent contribution and permutation importance for variables used as environmental predictors in the continuous model for the harpy eagle. All values are %.

Predictor	Percent contribution	Permutation importance
Evergreen forest (%)	71.2	34.9
Mean diurnal temperature range (°C)	12.9	19.1
Elevation (m)	5.6	15.1
Isothermality (%)	3.2	10.1
Precipitation wettest month (mm)	2.2	6.3
Cultivated (%)	1.7	5.0
Terrain Ruggedness Index (TRI)	1.5	2.9
Temperature seasonality (SD, °C)	1.3	5.8
Precipitation warmest quarter (mm)	0.3	1.0

Table S6.2. Geographical niche overlap calculated for predicted future distributions for the harpy eagle from 2030-2090 using three paleoclimate General Circulation Models (GCMs).

SSP245

Year	GCM	CanESM5	CNRM-ESM2
2030	CNRM-ESM2	0.948	
	MIROC-ES2L	0.941	0.967
2050	CNRM-ESM2	0.950	
	MIROC-ES2L	0.951	0.952
2070	CNRM-ESM2	0.937	
	MIROC-ES2L	0.942	0.953
2090	CNRM-ESM2	0.918	
	MIROC-ES2L	0.921	0.955

SSP585

Year	GCM	CanESM5	CNRM-ESM2
2030	CNRM-ESM2	0.937	
	MIROC-ES2L	0.943	0.956
2050	CNRM-ESM2	0.928	
	MIROC-ES2L	0.927	0.955
2070	CNRM-ESM2	0.908	
	MIROC-ES2L	0.908	0.944
2090	CNRM-ESM2	0.901	
	MIROC-ES2L	0.887	0.932

Table S6.3. Predicted change in future distribution area (km^2) for the harpy eagle using a lower emissions (SSP245) CMIP6 climate change scenario from three General Circulation Models (GCMs).

Year	GCM	Future area (km^2)	Loss or gain (km^2)	Loss or gain (%)
2030	CanESM5	7,318,047	-299,885	-3.9
	CRNM-ESM2-1	7,550,583	-67,350	-0.9
	MIROC-ES2L	7,566,312	-51,620	-0.7
	Mean	7,478,314	-139,618	-1.8
2050	CanESM5	6,882,584	-735,348	-9.7
	CRNM-ESM2-1	7,631,332	13,400	0.2
	MIROC-ES2L	7,232,711	-385,221	-5.1
	Mean	7,248,876	-369,056	-4.9
2070	CanESM5	6,588,509	-1,029,423	-13.5
	CRNM-ESM2-1	7,636,476	18,544	0.2
	MIROC-ES2L	7,197,029	-420,904	-5.5
	Mean	7,140,671	-477,261	-6.3
2090	CanESM5	6,034,912	-1,583,020	-20.8
	CRNM-ESM2-1	7,713,258	95,326	1.3
	MIROC-ES2L	7,445,726	-172,206	-2.3
	Mean	7,064,632	-553,300	-7.3

Table S6.4. Predicted change in future distribution area (km^2) for the harpy eagle using a higher emissions (SSP585) CMIP6 climate change scenario from three General Circulation Models (GCMs).

Year	GCM	Future area (km^2)	Loss or gain (km^2)	Loss or gain (%)
2030	CanESM5	6,651,210	-966,722	-12.7
	CRNM-ESM2-1	7,597,088	-20,844	-0.3
	MIROC-ES2L	7,376,030	241,902	-3.2
	Mean	7,208,109	-248,555	-5.4
2050	CanESM5	6,425,874	-1,192,058	-15.7
	CRNM-ESM2-1	7,598,186	-19,747	-0.3
	MIROC-ES2L	7,429,399	-188,533	-2.5
	Mean	7,151,153	-466,799	-6.1
2070	CanESM5	6,142,061	-1,475,871	-19.4
	CRNM-ESM2-1	7,565,340	-52,592	-0.7
	MIROC-ES2L	71,51,584	-466,348	-6.1
	Mean	6,952,995	-664,937	-8.7
2090	CanESM5	5,441,364	-2,176,568	-28.6
	CRNM-ESM2-1	7,261,414	-356,519	-4.7
	MIROC-ES2L	6,850,089	-767,843	-10.1
	Mean	6,517,622	-1,100,310	-14.4

Appendix 2 Supplementary Figures

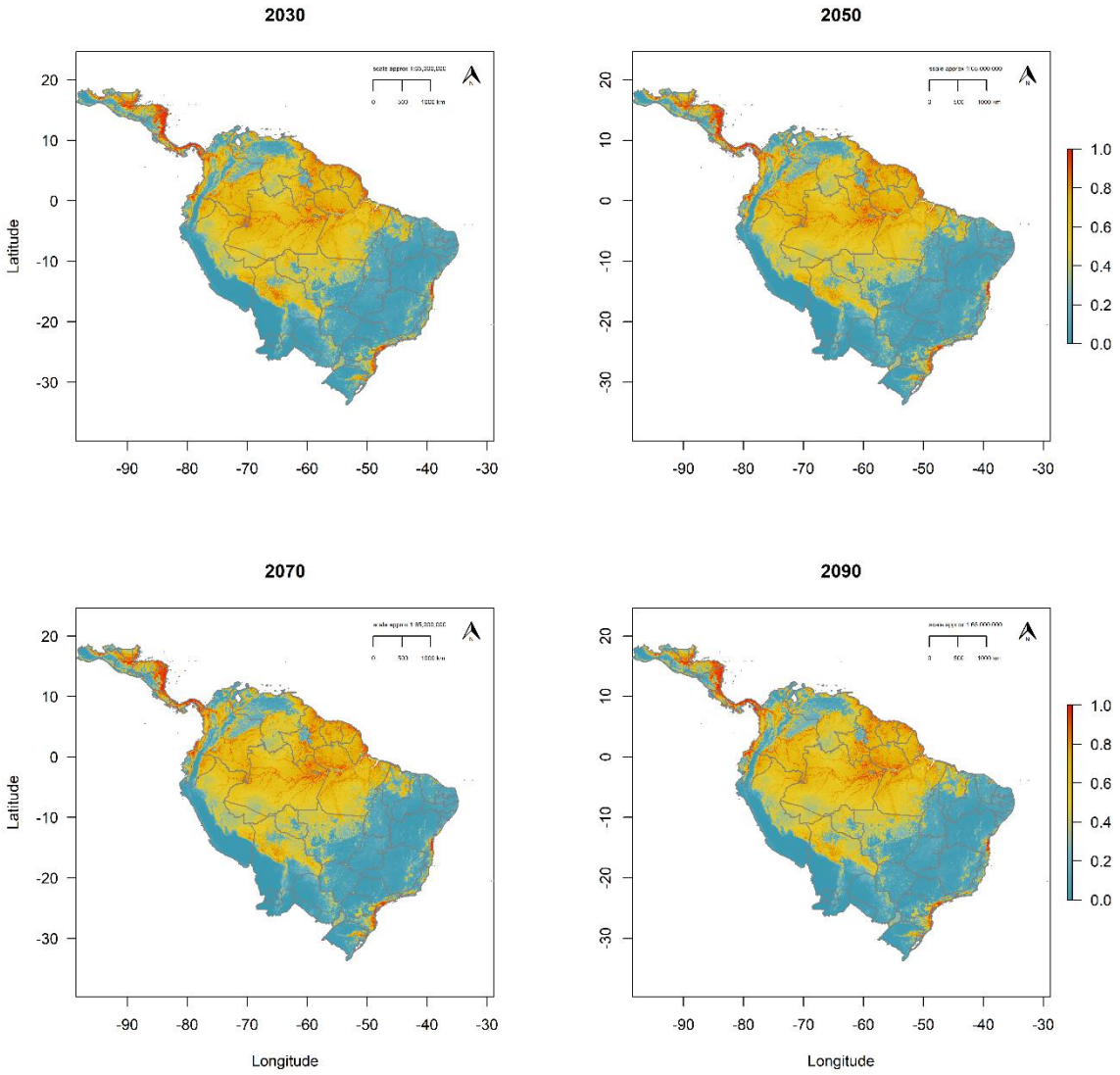


Figure S6.1. Continuous mean predictions from the three general circulation models for harpy eagle distribution using the SSP245 emissions scenario across four future climate change timeframes.

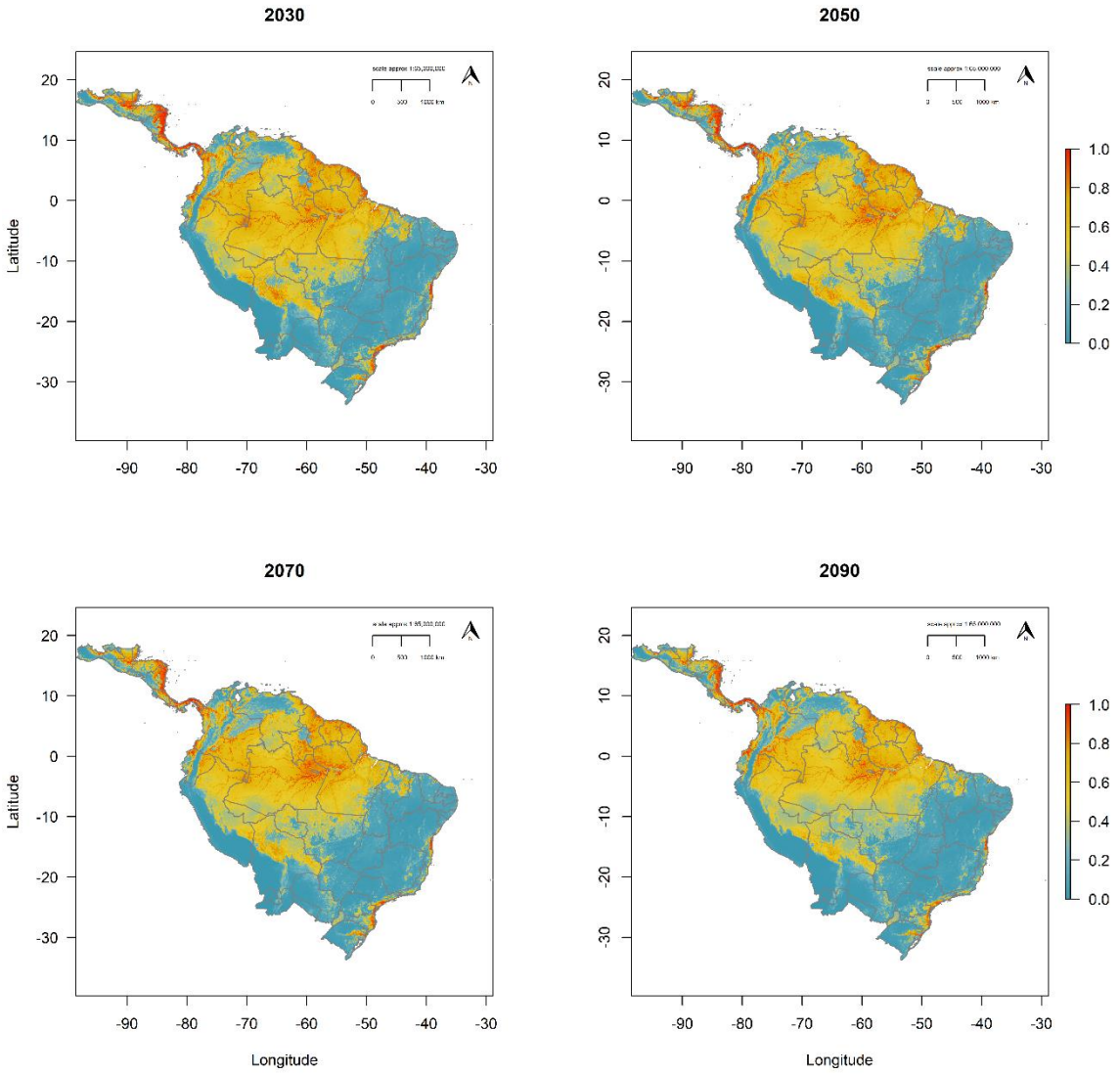


Figure S6.2. Continuous mean predictions from the three general circulation models for harpy eagle distribution using the SSP585 emissions scenario across four future climate change timeframes.

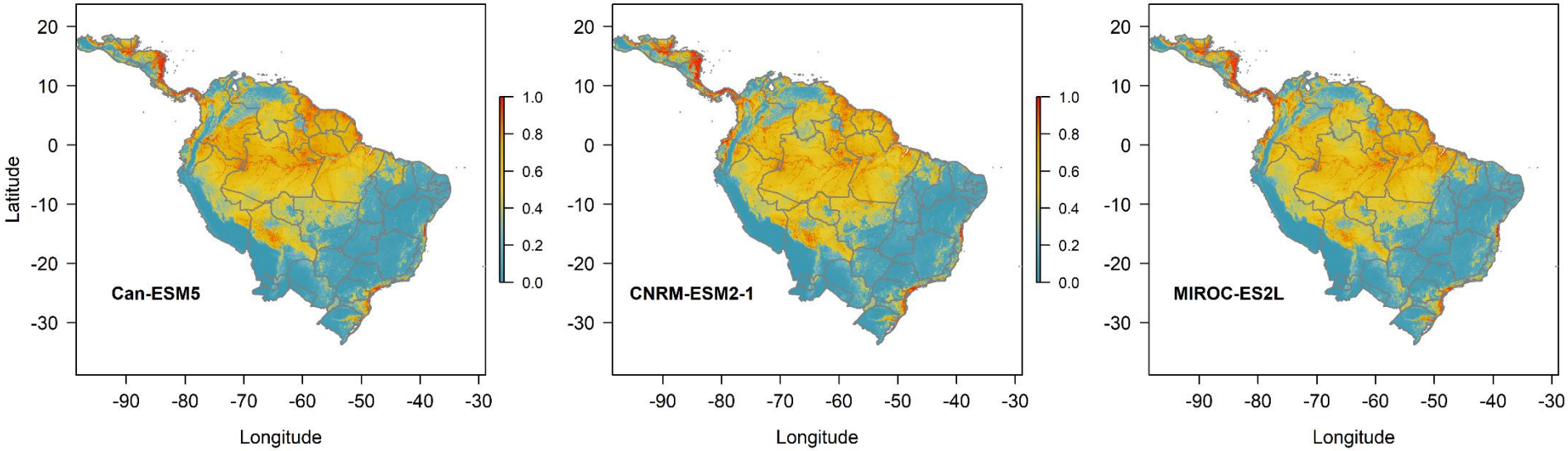


Figure S6.3. Predicted continuous future distribution for the harpy eagle across three Global Circulation Models for the year 2030 under a lower SSP245 carbon emissions scenario.

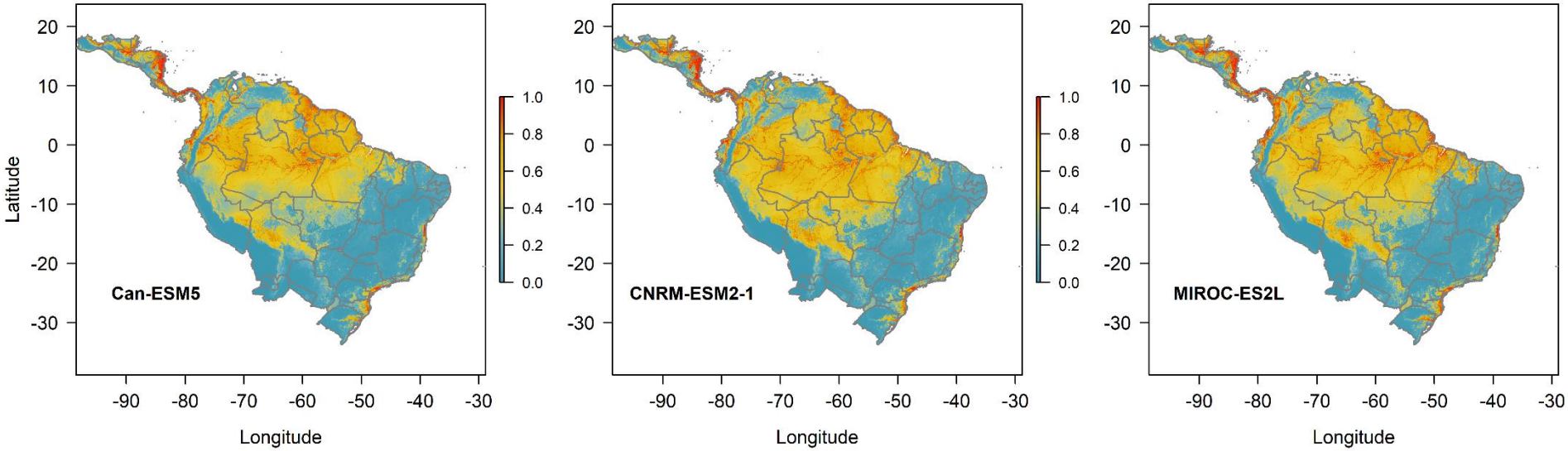


Figure S6.4. Predicted continuous future distribution for the harpy eagle across three Global Circulation Models for the year 2030 under a higher SSP585 carbon emissions scenario.

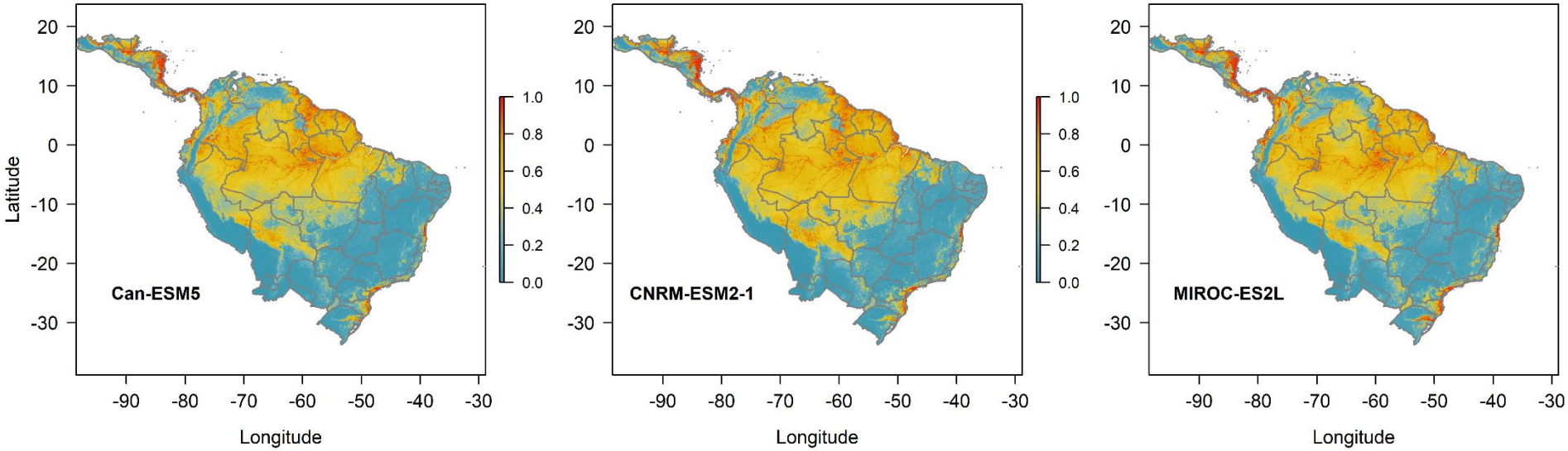


Figure S6.5. Predicted continuous future distribution for the harpy eagle across three Global Circulation Models for the year 2050 under a lower SSP245 carbon emissions scenario.

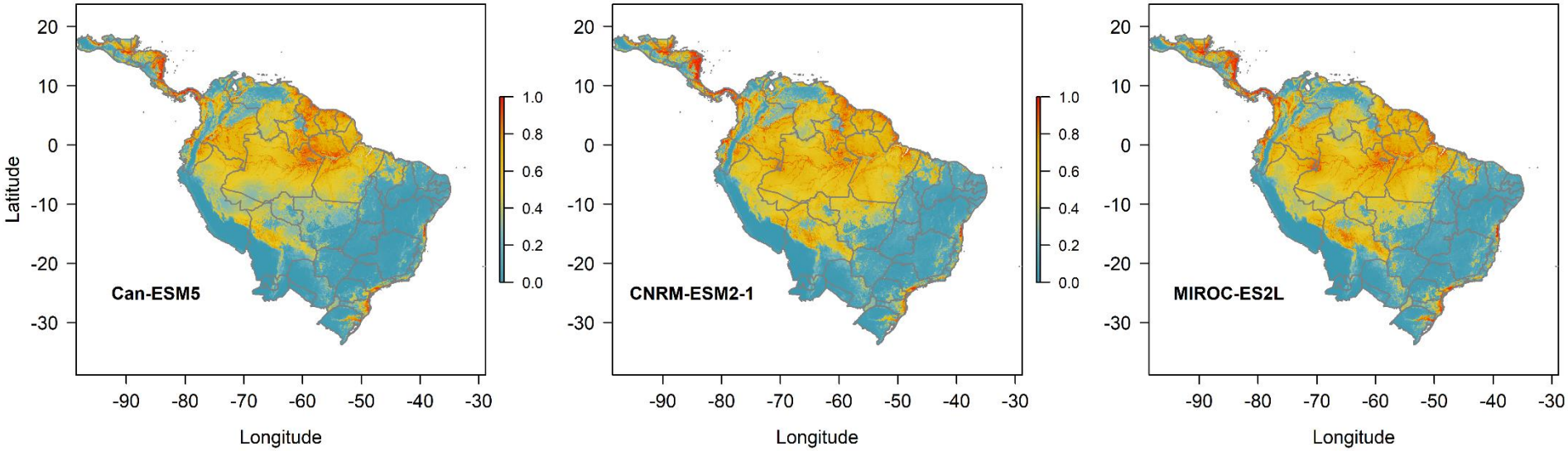


Figure S6.6. Predicted continuous future distribution for the harpy eagle across six Global Circulation Models for the year 2050 under a higher SSP585 carbon emissions scenario.

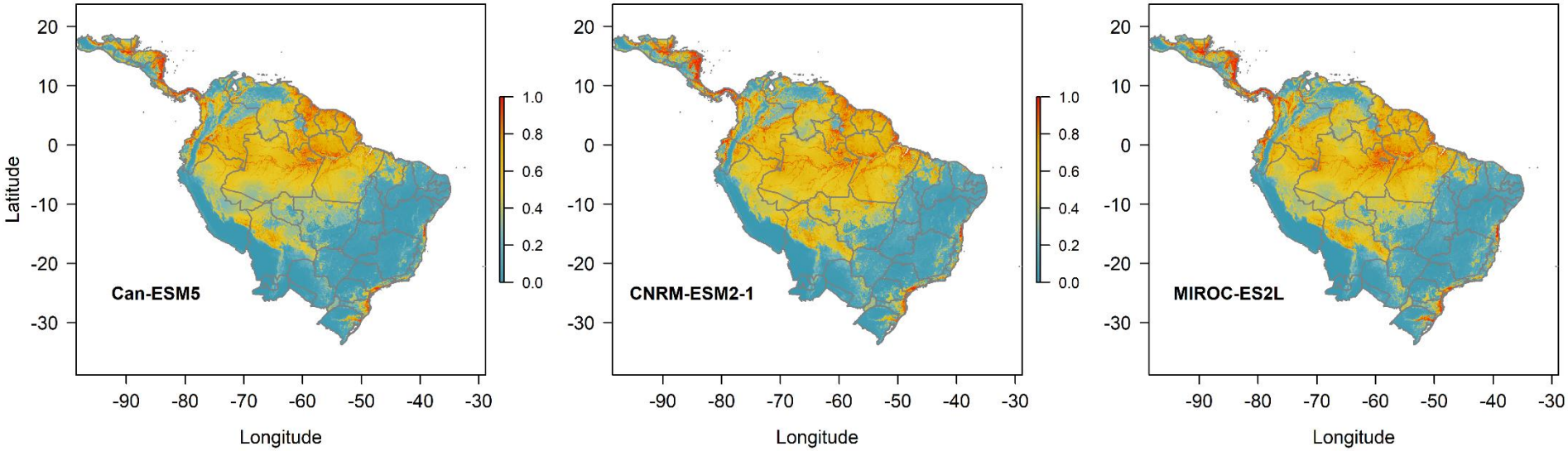


Figure S6.7. Predicted continuous future distribution for the harpy eagle across three Global Circulation Models for the year 2070 under a lower SSP245 carbon emissions scenario.

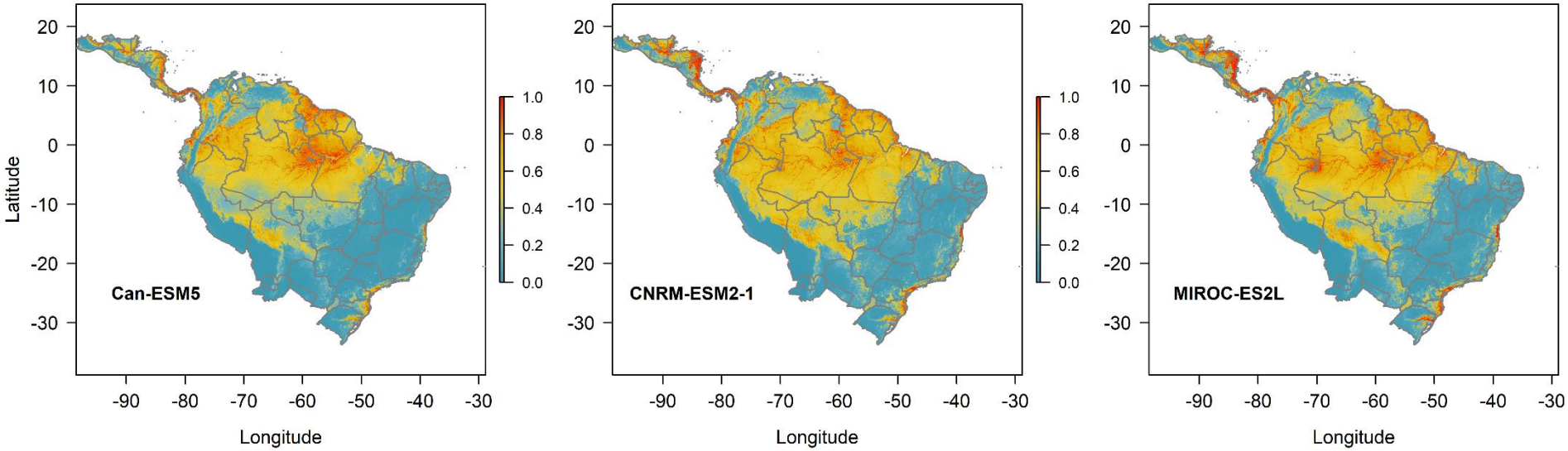


Figure S6.8. Predicted continuous future distribution for the harpy eagle across six Global Circulation Models for the year 2070 under a higher SSP585 carbon emissions scenario.

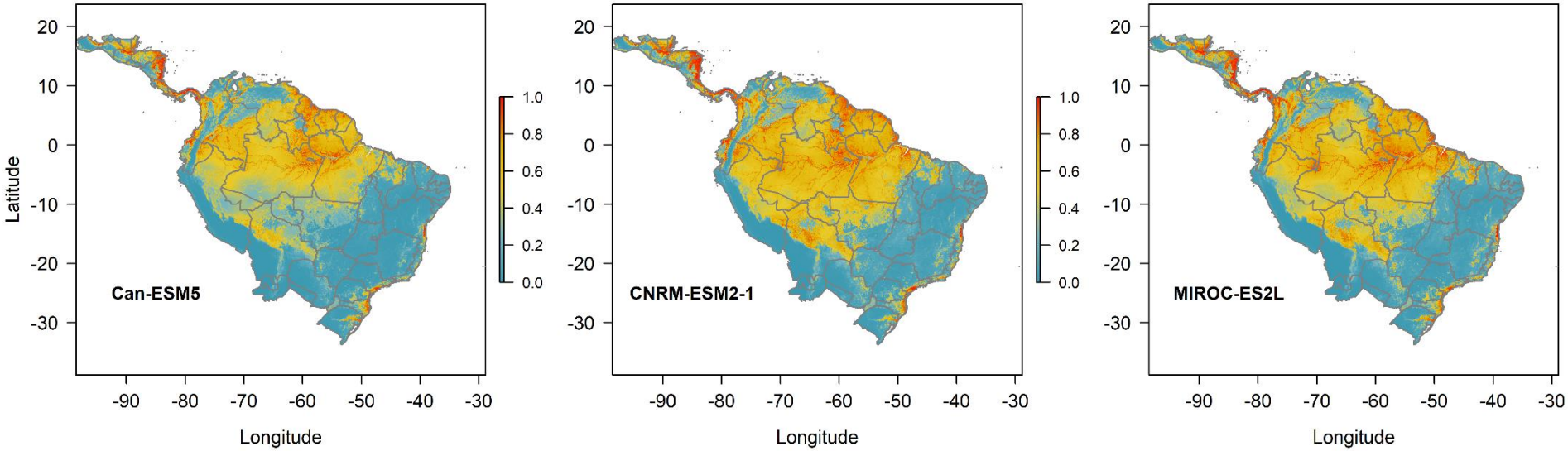


Figure S6.9. Predicted continuous future distribution for the harpy eagle across three Global Circulation Models for the year 2090 under a lower SSP245 carbon emissions scenario.

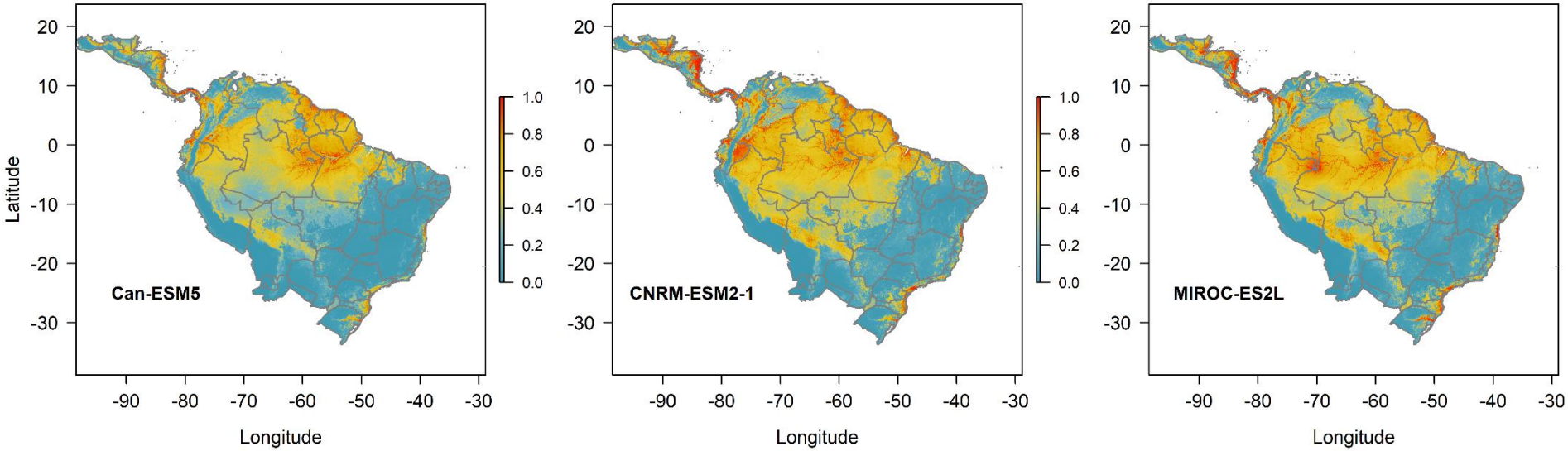


Figure S6.10. Predicted continuous future distribution for the harpy eagle across three Global Circulation Models for the year 2090 under a higher SSP585 carbon emissions scenario.

7. CONCLUSION

7.1 Summary

Identifying species distributions and ecological requirements is fundamental to understanding species range limits and setting spatial conservation planning priorities (Elith & Leathwick 2009a; Lawler *et al.* 2011). Here, I identified the current distributional constraints for the harpy eagle across its entire range using biotic, climatic, topographical, and landcover variables and predicted paleoclimatic and future distribution under past and expected future climate change scenarios. Applying this knowledge to long-term, broad-scale spatial conservation planning will help direct future designation and expansion of current protected area networks in line with suitable environmental areas now and into the future. Further, due to its reliance on lowland tropical forests the harpy eagle may act as a surrogate example, enabling greater understanding of how the range limits of an apex predator may point to how other tropical forest biota are predicted to respond to a changing climate (Urban *et al.* 2017).

The results presented here are reliant on the selected environmental covariates dependent on our definitions - animals may not experience the landscape as humans perceive it. Though I used a range of relevant abiotic and biotic predictors, including variables derived from satellite remote sensing, such as Normalized Differential Vegetation Index (NDVI; Pettorelli *et al.* 2005), and human impact (Human Footprint Index; Sanderson *et al.* 2002), would further build on the predictive ability of the SDMs presented here. Spatial models have much scope for improvement (Engler *et al.* 2017; Fourcade *et al.* 2017; Guisan *et al.* 2017), but ultimately may also be limited by the amount and quality of occurrence data required (Beck *et al.* 2014; Neate-Clegg *et al.* 2020).

Integrating multiple biodiversity data sources would seem a logical evolution for SDMs, particularly within a point process modelling (PPM) framework (Isaac *et al.* 2019). As shown throughout this thesis, the PPM framework using logistic regression via various models; generalized linear models (GLM), generalized additive models (GAM), and maximum entropy (MaxEnt), produces reliable and useful predictions for species range limits in the absence of detailed distributional information for a tropical forest raptor.

Few species occupy all areas with suitable resources and conditions, with areas of potential presence either occupied by closely related species, or unoccupied due to extinction or failure to disperse (Anderson *et al.* 2002). The results here show predictive models can identify those areas of highest environmental suitability, and where the main threats to at risk harpy eagle populations are concentrated. This then leads into where preventative conservation action would have the most benefit – not reactive conservation but proactive planning. The overall picture from all analyses is of highest habitat suitability, climate stability, and food resources in northern Amazonia and the Guiana shield, along with western Colombia, extending into eastern Panama. Thus, conservation efforts for the harpy eagle need extending beyond current programs to focus on these regions, some of which have seen little conservation action.

Improving our understanding of harpy eagle habitat use is especially relevant for conservation, because it may point towards potential population change and direct habitat management and protection. Across their range harpy eagles prefer evergreen forest cover between 70-75 %, which should be used as a minimum threshold for conserving tropical forest habitat. Developing a

collaborative working relationship with field researchers and land managers feeding back harpy eagle occurrence data would further improve habitat use assessments. In particular, locations of known nest sites would help identify the specific environmental breeding requirements for the harpy eagle, as the occurrence dataset used here is mainly comprised of sightings, with a smaller subset of additional nest locations. Given the broad range of the harpy eagle, any breeding habitat studies would be more effective at local, landscape scales (Vargas González *et al.* 2020). Moreover, developing a participatory modelling process (PMP; Ferraz *et al.* 2020), where researchers, planners and decision makers are all involved in the modelling process would be a significant step forward in harpy eagle conservation.

7.2 Future research

Areas under most human pressure (i.e. Central America, Brazil) have already seen harpy eagle population declines and extirpations, mainly through habitat loss (Vargas González *et al.* 2006). Regions such as Mato Grosso, on southern Brazil's agricultural frontier, and the Chocó-Darién ecoregion are now experiencing rapid deforestation (Hansen *et al.* 2008; Fagua *et al.* 2019) and are the regions which currently need most attention for harpy eagle conservation (Chapters 5 & 6). Historical population declines driven by habitat loss should serve as a forewarning for the future conservation status of the harpy eagle, as human-driven development progresses in these regions and elsewhere across the harpy eagle's broad range. Demographic response studies combined with Habitat Suitability Models are a promising method to further evaluate the relationship between population dynamics and habitat suitability (Bocedi *et al.* 2014). Further, modelling future distribution with both

predicted prey distributions and land cover change may also yield useful insights into the future conservation status for the harpy eagle.

Establishing protected areas is a critical component for strategies to counter biodiversity loss (Rodrigues & Cazalis 2020). Protected areas can be effective in maintaining biodiversity even if their coverage appears inadequate, with species abundance and diversity usually higher in protected areas (Rodrigues *et al.* 2004a). Thus, by protecting habitat for charismatic apex predators, whose habitat requirements include those of many other taxa, the harpy eagle may act as an umbrella or indicator species (Roberge & Angelstam 2004; Sergio *et al.* 2006), but this would require further testing. Indeed, sites occupied by raptors are more biodiverse than the surrounding areas lacking raptors (Sergio *et al.* 2005; Sergio *et al.* 2006), with consequently higher biodiversity representation in protected areas based on the presence of apex predators. Approximately 50 % of Important Bird and Biodiversity Areas (IBAs) have any type of formal protection (Donald *et al.* 2019). Therefore, use of spatial conservation planning software (i.e., Zonation; Lehtomäki & Moilanen 2013) would also help identify the most cost-effective areas to purchase land for IBAs and connect habitats, where there is currently limited protected area coverage but with high habitat suitability.

The harpy eagle has a continental range, but as demonstrated in this thesis, the species has a discontinuous range restricted to specific vegetation types. Probably the main reason for such a large range must be the extensive area of lowland tropical forest across the Neotropics. Remoteness and inaccessibility of lowland tropical forest may be the main reason many harpy eagle populations

still persist. However, with habitat loss driven by deforestation predicted to increase across the more remote parts of the harpy eagle range (Powers & Jetz 2019), identifying the potential distribution of at-risk harpy eagle populations at a finer scale is required to direct conservation action and assess localized extinction risk. The gaps in the IBA network should be urgent priorities for finer-scale analyses building on the broad-scale models here. In particular, the Guiana shield is a priority area for research. The region had high suitability in all models but is a neglected region in terms of both research and conservation.

Species ranges have an invariably discontinuous spatial arrangement, and this most likely applies to all taxa if mapped at fine scales (Ladle & Whittaker 2011). In the absence of human disturbance, discontinuous distributions are a consequence of patchy environments, so it follows that species ranges will follow the latter (Riddle *et al.* 2011). Range occupancy is also scale dependent, with varying scales of spatial pattern in individual species (Levin 1992; Garshelis 2000). Refining broad scale modelling to localized regional studies would be a logical next step. Exploratory ground-truthing surveys to validate the models would also be of benefit to conservation managers and modellers alike. Many developing tropical countries lack extensive resources for biodiversity management but are generally the regions of the planet with highest biodiversity. Vast wilderness areas make systematic sampling for many species almost impossible, and that is where spatial models are required to fill knowledge gaps and determine potential distributional areas as demonstrated throughout this thesis.

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